
THE ORIGIN OF GRASS-DOMINATED ECOSYSTEMS¹

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ABSTRACT

Approximately one-third of the Earth's vegetative cover comprises savannas, grasslands, and other grass-dominated ecosystems. Paleobotanical, paleofaunal, and stable carbon isotope records suggest five major phases in the origin of grass-dominated ecosystems: (1) the late Maastrichtian (or Paleocene) origin of Poaceae; (2) the opening of Paleocene and Eocene forested environments in the early to middle Tertiary; (3) an increase in the abundance of C₃ grasses during the middle Tertiary; (4) the origin of C₄ grasses in the middle Miocene; and (5) the spread of C₄ grass-dominated ecosystems at the expense of C₃ vegetation in the late Miocene. Grasses are known from all continents except Antarctica between the early Paleocene and middle Eocene. Herbivore morphology indicative of grazing, and therefore suggestive of grass-dominated ecosystems, appears in South America by the Eocene-Oligocene boundary, prior to the occurrence of grazing morphology elsewhere, and persists throughout the Cenozoic. Clear vertebrate and paleobotanical evidence of widespread grass-dominated ecosystems in northern continents does not occur until the early to middle Miocene. C₄ grasses are present from approximately 15 Ma and undergo a dramatic expansion in the lower latitudes of North America, South America, East Africa, and Pakistan between 9 and 4 Ma. The expansion may have taken place in a shorter interval in some regions. C₄ grasses are characteristic of seasonal, arid, and warm environments and are more tolerant of lower atmospheric CO₂ (< 400 ppmv) than C₃ plants. C₄ grass distribution, therefore, is climatically controlled. The late Miocene spread of C₄ grasses possibly involved a decrease in atmospheric CO₂ and heralded the establishment of modern seasonality and rainfall patterns.

Grass-dominated ecosystems, savannas and natural grasslands, comprise about one-third of the Earth's vegetative cover (Fig. 1, Shantz, 1954). In addition, grasslands and savannas are highly productive, supporting vast numbers of mammalian herbivores and an associated fauna. Humans depend upon domesticated grasses, especially corn, wheat, and rice, to support a burgeoning world population through direct consumption of grain and through animal husbandry built upon grasses. As a consequence, extensive areas of once natural grasslands and savannas have been converted to agricultural uses. It follows that ecological study of natural grasslands and savannas is essential not only for their management and conservation, but also because of their relevance to agriculture. Paleoecology provides a framework for understanding the original development of grass-dominated ecosystems, the basis of their plant-animal interactions, and their role in human evolution. Moreover, because the modern distribution of grassland and savanna biomes is correlated with specific climatic

parameters, their origins are linked to global climate evolution.

Our purpose is to address the origin of grass-dominated ecosystems by reviewing evidence from the paleobotanical, vertebrate paleontological, and stable carbon isotope records. It is meant to provide an adequate and reasonably thorough, but not exhaustive, coverage of the literature pertaining to each continental region with a focus on those geographic areas that are most informative with respect to the fossil or isotope records. We aim to answer the following questions: When do grass-dominated ecosystems first appear on each of the continents studied? Is the first appearance of grass-dominated ecosystems synchronous worldwide? Do the paleobotanical, paleofaunal, and stable carbon isotope data yield concordant evidence with respect to the origin of grass-dominated ecosystems for specific time intervals and regions?

There are a variety of grass-dominated ecosystems. Savannas are tropical and subtropical grass-dominated landscapes with varying densities of

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trees and shrubs. Density of the woody component and species composition are sensitive to a complex of factors including climate, soil, and disturbances such as fires, human land use practices, and grazing pressure (Pratt et al., 1966; Bourlière & Hadley, 1983; Cole, 1986; Morell, 1997). Savannas exhibit a range of physiognomic forms such as grass savanna (in which trees and shrubs are absent), bushland and thicket, shrubland, tree savanna, and wooded savanna (Boughey, 1957; White, 1983). Menaut (1983), based on work in Africa, recognized a more inclusive savanna biome, restricted to the tropics and subtropics, but within which are found all variants between desert and forest. For the purposes of this paper, the most important part of any definition of savanna is the key phrase, "grass-dominated." Savannas are found today where precipitation is seasonal, if not monsoonal. Rainfall varies widely from as little as 500 mm/year over one to two months, to as much as 1500 mm/year with a short dry season (Bourlière & Hadley, 1983).

Temperate grasslands, as opposed to savannas, are found in middle latitudes or at upper elevations where precipitation is too scant to support tree growth, but greater than that resulting in deserts (Ripley, 1992). As with savannas, grassland climates are seasonal and have a wide range in mean annual precipitation, between about 500 and 1500 mm/year (Ripley, 1992). Typically, temperate grasslands are nearly continuous expanses of grasses and sedges without trees, but including small shrubs and varying amounts of herbaceous dicots (Coupland, 1992a). However, similar to savannas, grasslands vary in species composition and physiognomy depending on variations in climate, soil, topography, and land use. For example, in cold, dry, continental interiors, grass and shrubs form the grassland variant known as steppe.

Traditionally, the primary means of recognizing and evaluating grass-dominated ecosystems in the paleontological past was through the interpretation of the mode of life of fossil vertebrates. The evolution of horses has played a central and deserved role in interpreting the origin of grass-dominated ecosystems because of the high-crowned teeth characteristic of Miocene and later members of the horse family Equidae, the grazing habits of the living species, their dispersal history, and the high quality of their fossil record (e.g., Kowalevsky, 1873; Osborn, 1910; and many good reviews of the subject including Simpson, 1951, 1953; Webb, 1977; MacFadden, 1992). Improvements in the paleobotanical record (both macrofossil and pollen) provide a more direct route to plant communities of the past (Elias, 1942; Thomasson, 1979; Morley

& Richards, 1993). A third approach is the assessment of stable carbon isotopes in fossil material such as herbivore enamel and in paleosol components that yield information on the photosynthetic pathways of vegetation in ancient ecosystems (Cerling, 1984; Quade et al., 1989a; Kingston et al., 1994; Morgan et al., 1994). Together these disciplines provide a robust means of evaluating the origin of grass-dominated ecosystems.

The continents of North America, Eurasia, South America, Africa, and Australia are reviewed for relevant paleontological and stable carbon isotope data. The record starts in each region with the earliest documented occurrence of grass, which provides a maximum potential age for the origin of grass-dominated ecosystems for that particular region. We use published age estimates. If improvements in an age assignment have been made, we use the revised estimate as indicated in our text.

Consideration must be given separately to the strengths and weaknesses in the quality of the paleobotanical, paleofaunal, and isotopic records, and to the individual development of these lines of evidence on each continent. First we will address aspects of the paleobotanical, paleofaunal, and isotopic records that relate to grasses in terrestrial biomes; then we will review the records for each continent beginning with a summary of all three lines of evidence for each region.

THE PALEOBOTANICAL RECORD

Grass pollen is much more common in the Tertiary paleobotanical record than grass macrofossils. Grasses are primarily wind pollinated, and therefore they produce copious amounts of pollen that can be carried long distances by wind and water, as evidenced by grass pollen in marine cores. Pollen provides a regional view of vegetation. Unfortunately, grass pollen is fairly uniform throughout the family precluding identification at lower taxonomic levels.

Maastrichtian and early Tertiary grass pollen is identified as the form taxon, *Monoporites annulatus* van der Hammen (= *Graminidites* I. C. Cookson ex R. Potonié). The botanical name describes the single pore surrounded by a thickening, or annulus, that characterizes the pollen in all species of the grass family. However, the five or six other small families in the order Poales (Linder, 1986) also have a single pore, some with an annulus (Linder & Ferguson, 1985). Although the presence of fine channels in the pollen wall and absence of scrobiculae (minute pits in the wall) distinguish grass pollen, the fine channels can only be seen with

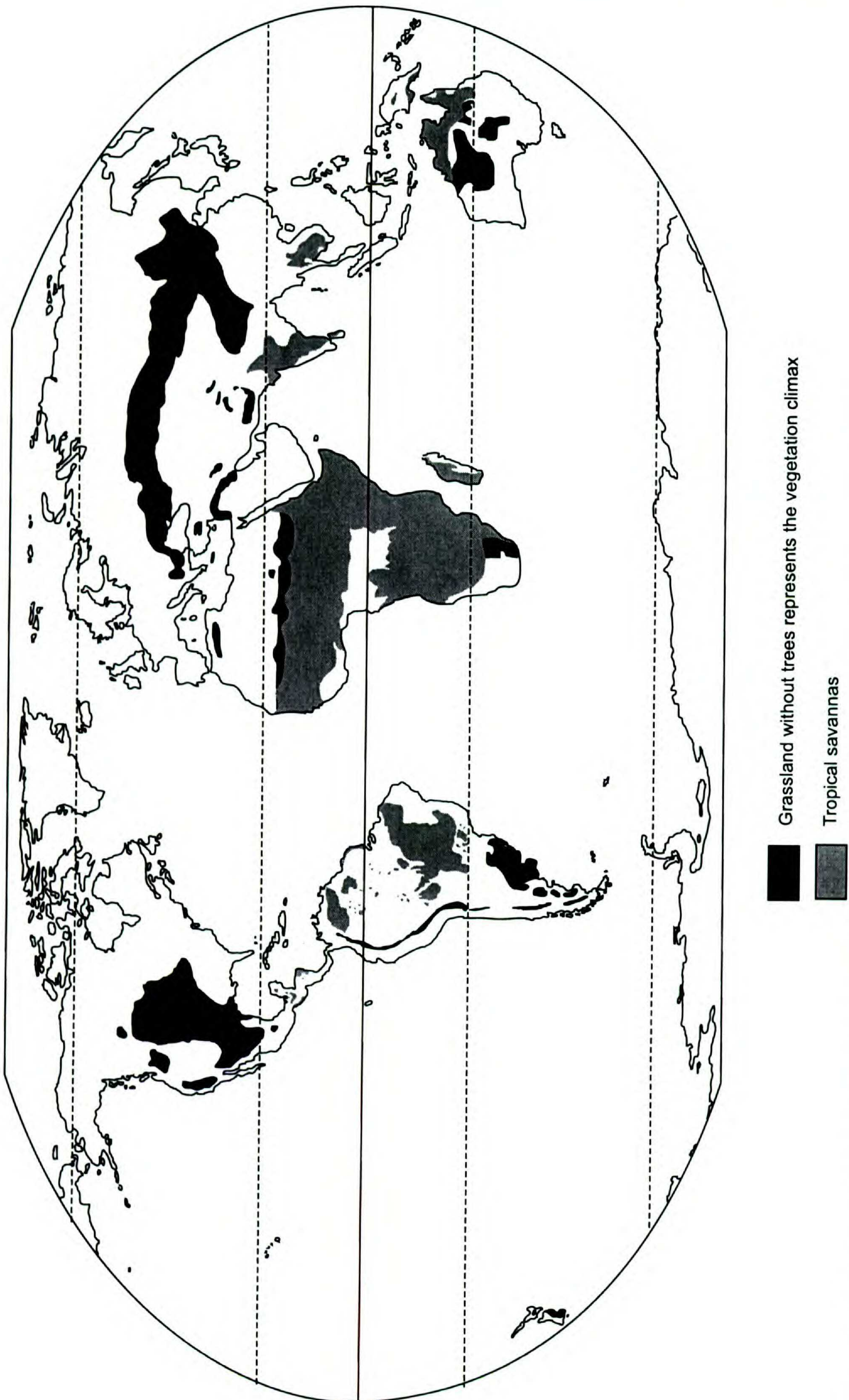


Figure 1. Modern distribution of grass-dominated ecosystems. Redrawn from Bourlière & Hadley (1983) and Coupland (1992d).

transmission electron microscopy, a technique not used routinely in pollen identification. Thus, the re-evaluation and recognition of scrobiculae in some Maastrichtian and Paleocene pollen grains that originally were identified as *Monoporites annulatus* led to their reassignment to families other than Poaceae. This calls into question other early grass pollen identifications that have not been similarly re-evaluated (Muller, 1981; Linder, 1986). Nevertheless, Linder (1986) accepted at least some of the Maastrichtian identifications of *Monoporites annulatus* from Egypt as valid (Kedves, 1971), and more recent studies in northern South America document frequent occurrence (no quantitative data supplied) of *Monoporites annulatus* in the early Paleocene (Muller et al., 1987). Undoubted grass macrofossils occur in the early Eocene Claiborne Formation of Tennessee (Crepet & Feldman, 1991; Crepet & Herendeen, 1992), although no further age refinement was supplied, confirming the presence of Poaceae by at least the early Tertiary. The grass pollen record is well established with the consistent occurrence of *Monoporites annulatus* after the middle to late Eocene, especially in tropical regions (see discussions for South America and Africa below).

Palynological publications reviewed here report abundance data either categorically (rare, frequent, or common), as relative percentages, or simply as present or absent. If no paleoenvironmental interpretation is provided by the author(s), where possible the record is interpreted here. Leopold et al. (1992) compiled data from studies of grass pollen in modern soils to serve as a coarse guide to the paleoenvironmental significance of fossil grass pollen percentages. Grass pollen percentages from modern soils of steppe, grassland, and savanna environments vary widely: from 1% to 25% in Wyoming steppe, to 20% to 55% in Ethiopian savanna. To make the most reasonable interpretation of fossil pollen assemblages, the abundance and composition of associated non-grass pollen taxa are also considered.

Grass phytoliths are the opaline silica remains of silica cells (silica bodies) deposited mainly in the leaf epidermis. Silica bodies vary in shape, even on the same leaf, but generally grass subfamilies are recognized as having characteristic silica bodies. Consequently, phytoliths found in ancient soils may document past changes in grass composition at the subfamily level (Fredlund & Tieszen, 1997).

Grass macrofossils provide greater taxonomic resolution than pollen because of taxonomically diagnostic characters that facilitate broad comparisons and phylogenetic studies. Grass leaves are not

shed but remain on the plant, even after death. Therefore, grass leaves in non-aquatic settings are not likely to become part of the sedimentary record. Grass reproductive structures are often adapted for dispersal by wind or animals, separating readily from the parent plant, and more commonly enter the fossil record. North America has a unique and spectacular record of fossil grass reproductive parts replaced by silica and calcium carbonate (Thomasson, 1990), as opposed to the poor record of leaves.

THE PALEOFAUNAL RECORD

Mammals are a diverse group of species with a wide range of morphological and behavioral adaptations (Eisenberg, 1981). Herbivorous mammals play a fundamental role in the recycling of nutrients in the ecosystem by processing food through their digestive systems, by becoming prey, by trampling vegetation into the soil, or by other behaviors (McNaughton et al., 1988). They are major influences on plant and ecosystem physiognomy, as is readily observed by the destruction of trees by elephants in Africa (McNaughton et al., 1988; Dublin, 1995), for example, or less apparently by the actions of small mammal herbivores, such as the pruning of picturesque junipers by packrats in the American Southwest (Vaughan, 1980). Coevolutionary relationships between herbivores and plants are reflected by adaptations for processing and digesting vegetation exhibited by herbivores and the attributes of plants that limit their digestibility or palatability (McNaughton et al., 1985; Vicari & Bazely, 1993; Seldal et al., 1994; Karban & Baldwin, 1997). In short, herbivores help to create the environment in which they live.

The most directly relevant mammalian herbivores for recognizing grass-dominated ecosystems based on morphological adaptations are derived ungulates, a large suite of hoofed mammals that includes equids. Derived ungulates have limbs modified such that the body weight is borne by the last joints of the digits, the ungual phalanges. The most useful ungulate groups are the perissodactyls (most notably horses, rhinoceroses, and their relatives) and the ruminant artiodactyls (Janis & Scott, 1987), which in the modern fauna include mouse deer or chevrotains (Tragulidae), giraffe and okapi (Girafidae), musk deer (Moschidae), deer and muntjacs (Cervidae), pronghorn (Antilocapridae), and cattle, antelope, bison, duikers, and goats (Bovidae). The role of ungulates in South America throughout the Tertiary was filled by endemic groups, e.g., notungulates. The mammalian herbivore fauna of Australia

lia was effectively comprised of marsupials, such as kangaroos, during the Tertiary.

The interpretation of past grass-dominated ecosystems relies most heavily on ungulates because they rely directly on plants for food, they exhibit recognizable adaptations associated with diet, they have an abundant fossil record, and their utility has been more thoroughly tested than in other groups. Their long legs are suited for running, an adaptation for life in open environments. Living ungulates provide models for interpreting the ecology of more obscure, extinct ungulate groups, such as the unfamiliar herbivores characteristic of the South American Tertiary (MacFadden, 1997).

Mammalian carnivores may provide additional indications of habitat, such as cursorial adaptations associated with the pursuit of fleet prey species inhabiting open country (Hunt & Solounias, 1991; Van Valkenburgh, 1985; Van Valkenburgh & Janis, 1993; Werdelin & Solounias, 1996). Among non-mammalian groups, snakes, for example, which are cold-blooded predators, have a fossil record that seems to parallel the achievement of grass-dominated ecosystems in North America (Parmley & Holman, 1995). This link presumably reflects the complex ecological connections among evolving climate, changing habitat, and the adaptations of their prey, which consists in large part of small mammal herbivores (rodents). None of these groups, however, has the demonstrably close link to grass and grass-dominated ecosystems exhibited by ungulates.

Recently, the study of ungulate paleoecology has been revitalized, providing a theoretical and quantitative basis for evaluating the feeding strategies of extinct herbivores (see review by Janis, 1995). Grazers are defined as herbivores whose year-round diets comprise 90% grass; browsers consume less than 10% grass; and mixed-feeders fall somewhere in between. These appear to be realistic categories defined by observation of extant ungulates and correlated with stomach anatomy (Hofmann & Stewart, 1972; Hofmann, 1973). Recognition of these dietary categories in the fossil record is based primarily on anatomical features of the teeth, premaxilla, and maxilla, and on microwear patterns in tooth enamel caused by abrasion during the chewing of food (Walker et al., 1978; Janis & Ehrhardt, 1988; Solounias et al., 1995b).

Grazers usually have teeth with high crowns, providing long-wearing ridges of enamel for the mastication of fibrous and tough food. Such high-crowned or rootless and ever-growing (hypselodont or hypselodont) teeth are relatively common among mammalian taxa, occurring in about half of the 34

orders, in species of a variety of body sizes, and with a wide range of diets (White, 1959; Janis & Fortelius, 1988). Janis (1988) determined that the amount of grit or other abrasive material ingested with food is the most important factor in predicting hypsodonty in ungulates, and thus explained why hypsodonty is not limited to grazers, as for example in the pronghorn or the Miocene stenomyline camels. It is conceivable but not proven that grass and grazing may play coevolutionary roles in the development of hypsodonty with grass responding to cropping by increasing the amount of silica (McNaughton & Tarrants, 1983; McNaughton et al., 1985; Vicari & Bazely, 1993; Karban & Baldwin, 1997), which, in turn, may select for high-crowned teeth in grazers (Van Valen, 1960; Janis & Fortelius, 1988).

Uncertainty of the significance for grazing of high-crowned teeth in individual cases is minimized when other morphological features of the species are taken into account. Grazers have square, straight premaxillae and broad muzzles; browsers have narrow muzzles; mixed-feeders fall in between (Janis & Ehrhardt, 1988; Solounias & Moelleken, 1993a, b; Dompierre & Churcher, 1996). In addition, grazers have relatively larger masseteric chewing musculature than mixed-feeders and browsers, which can be ascertained from the morphology of the jaw (Solounias et al., 1995b). Furthermore, diets can be evaluated by scanning electron microscopy of wear surfaces on teeth, grazing leaving a quantifiably different pattern of microwear on teeth compared to browsing, and mixed-feeders having elements of both patterns (e.g., Solounias et al., 1988). However, "the Last Supper Syndrome," in which rapid wear betrays previous microwear patterns, leaving only a reflection of the most recent meals, may well introduce a bias if the final meals of an animal do not accurately reflect the food preferences or normal diet of the species (Solounias et al., 1994).

As with ungulates, the skeletal and dental adaptations of small mammals are of use in interpreting open and grassland environments. The high-crowned dentition of voles and their African ecological counterparts, the groove-toothed rats, allows for mastication of fibrous, relatively low-nutrition food (Rensberger, 1973, 1975, 1978; Butler, 1980). In contrast, modern beavers have high-crowned teeth, but they also have a diet of bark with no relevance for the origin of grass-dominated ecosystems. The situation is less clear when Miocene beavers, some of which burrowed, are taken into account (Korth, 1994). Rodents and other small mammals may exhibit other adaptive fea-

tures, such as ricochetal locomotion, that are reflected in the skeleton and are indicative of open environments (Lyon, 1901; Hatt, 1932; Howell, 1932). The bipedal adaptations in jerboas, the most extremely adapted ricochetal rodents, have developed to the extent that the fused foot bones (metatarsus) are convergent with the tarsometatarsus of birds (Rich, 1973). Size is correlated with many facets of the natural history of a species, including home range (McNab, 1963; Western, 1979), which is much smaller for a rodent than for a long-legged ungulate, and the area required for foraging is less. Therefore, information regarding the distribution of open habitats provided by large versus small mammals may not be comparable in scale.

Given that the adaptations of individual species reflect habitat, then the suite of mammalian species found in a region and the resulting community structure should provide a more robust reflection of the environment than the adaptations of any particular species alone. Thus, by comparison with modern assemblages from known habitats, a fossil assemblage can be used to evaluate ecosystems and the roles of the component species of the past (Andrews & Van Couvering, 1975; Andrews et al., 1997). The pattern of changing species composition within assemblages over time should reflect changing environmental parameters or other factors that affect species distribution (Barry et al., 1985; Janis, 1984, 1988, 1993; Legendre, 1987), demonstrating open versus closed habitats, or a preponderance of grazers versus browsers and mixed-feeders. Grass-dominated ecosystems containing trees and shrubs support a more diverse fauna than pure grasslands because browsers and mixed-feeders are included in the community (Bourlière, 1963).

The paleofaunal record can be compared to the plant fossil record to discern patterns of coevolution assessed by coincident changes in both records that appear ecologically correlated. Examples include the evolutionary relationship between large nuts and rodents, or primates and fleshy fruits, both appearing in the early Tertiary (Collinson & Hooker, 1987, 1991; see also Wing & Tiffney, 1987), or between grass fossils and mammals as is reviewed here. More direct evidence of herbivore diet, and therefore indications of the relative importance of grass to a species, is obtained by analysis of the animal, as discussed above, or by the ratio of stable isotopes in fossils (e.g., Koch et al., 1994, 1995; Morgan et al., 1994; MacFadden, 1998; MacFadden & Cerling, 1996; MacFadden & Shockey, 1997), as discussed below.

THE ISOTOPIC RECORD

Recognition and characterization of biogeochemical cycles that mediate distribution of light stable isotopes (C, O, H, and N) in terrestrial ecosystems have contributed substantially to reconstructions of past environments. The relative abundance of two naturally occurring stable isotopes of carbon (^{12}C and ^{13}C) in fossils and paleosols has proved particularly useful in reconstructing aspects of the vegetation. The premise underlying this approach is that the tissue of plants utilizing alternative photosynthetic pathways can be differentiated on the basis of the ratio of $^{13}\text{C}/^{12}\text{C}$. This isotopic signature can be retrieved from the fossil record, either by direct analysis of ancient organic residues or from inorganic material that formed in isotopic equilibrium with the paleovegetation.

Terrestrial plants assimilate carbon from the atmospheric CO_2 reservoir by one of three photosynthetic pathways. These pathways, referred to as C_3 (Calvin-Benson), C_4 (Hatch-Slack or Kranz), and CAM (Crassulacean Acid Metabolism), represent adaptations to variable atmospheric and climatic conditions. In all three pathways, during the first stage of photosynthesis (carboxylation), carbon incorporated into the organic plant matrix is significantly depleted in the heavy isotope (^{13}C) relative to atmospheric CO_2 (Craig, 1953; Park & Epstein, 1960; Smith & Epstein, 1971; O'Leary, 1981; Farquhar et al., 1982). This discrimination against ^{13}C (fractionation) is due to small differences in physical and chemical properties imparted by the difference in mass between ^{12}C and ^{13}C . The extent to which fractionation occurs varies significantly depending on the pathway utilized. C_3 plants are most depleted, whereas plants endowed with the C_4 metabolic pathway are least depleted. There is a distinct non-overlapping bimodal distribution of the isotopic composition (denoted as $\delta^{13}\text{C}$) of C_3 versus C_4 plants. Plants that fix CO_2 by CAM display intermediate isotope values overlapping the range of both C_3 and C_4 flora (O'Leary, 1988).

C_3 plants dominate terrestrial environments and account for approximately 85% of all plant species, including almost all trees and shrubs as well as high-latitude or high-altitude grasses preferring wet, cool growing seasons. Environmental influences affecting the isotopic composition of C_3 plants include water stress, nutrient availability, light intensity, CO_2 partial pressure, atmospheric $\delta^{13}\text{C}$, temperature, and extent of forest canopy (Farquhar et al., 1982; van der Merwe & Medina, 1989; Tieszen, 1991). These environmental factors, coupled with genetic differences, result in substantial stable

carbon isotopic variation in C_3 vegetation that should be considered in attempting to document the relative amount of C_3 vegetation in a past ecosystem.

Although C_4 physiology is present in a number of monocots and diverse dicots, the bulk of C_4 global biomass is represented by graminoids, especially grasses growing in hot, arid habitats (Ehleringer et al., 1997). Modern C_4 -dominated ecosystems include tropical savannas, temperate grasslands lower than about 37° latitude, and desert scrubland. The C_4 photosynthetic pathway represents a modification of the C_3 mechanism and is considered to have evolved independently at least 26 times among the plant families that have it (Peisker, 1986), at least 5 times within the grass family itself (Renvoize & Clayton, 1992; Sinha & Kellogg, 1996). In C_4 plants, CO_2 is fixed initially in mesophyll cells as a 4-carbon compound that is transported to bundle sheath cells and then enters the C_3 pathway. The internal concentration of CO_2 in the bundle sheath cells is much greater (> 2000 ppmv) than atmospheric CO_2 thereby reducing the loss of C to photorespiration and increasing the overall efficiency of photosynthesis. C_4 plants generally tolerate higher temperatures and solar irradiance, drier conditions, greater seasonality, and lower atmospheric p CO_2 levels than C_3 species. C_4 photosynthesis, however, is energetically more costly (Salisbury & Ross, 1985), and C_4 species are outcompeted by C_3 plants at mean maximum temperatures below $25^\circ C$ and at higher p CO_2 levels (400 ppmv). In tropical to subtropical regions there is an altitudinal transition from C_4 to C_3 grasses between 2000 and 3000 m (Tieszen et al., 1979). Grasses in closed canopy forests in these regions are C_3 except where the canopy is broken.

Crassulacean acid metabolism (CAM) evolved independently in many succulent plants including the cacti (Cactaceae) and stonecrops (Crassulaceae). CAM plants may fix atmospheric CO_2 via the C_3 pathway or in a time-separated sequence similar to C_4 pathway in which CO_2 is fixed at night (when the temperature and humidity are lower) and is photosynthesized during the day (when light levels are higher). The extent to which each pathway is utilized depends on environmental conditions, resulting in a range of $\delta^{13}C$ values spanning that of C_3 and C_4 plants (O'Leary, 1981; Deines, 1980). Under high light intensity or high temperatures, CAM vegetation has $\delta^{13}C$ values similar to C_4 , whereas under environmental conditions of low light intensity and cold temperatures, they exhibit values similar to C_3 . The strategy of CAM plant physiology to endure extremely xeric conditions se-

verely limits their ability to take in and fix CO_2 , and in general, the net photosynthetic rate is much lower than C_3 or C_4 plants. In modern ecosystems, ungulates specializing on CAM succulents are rare, and we assume this to be the case in the past as well.

As the C_3 and C_4 photosynthetic pathways are associated with different environmental conditions and often plant physiognomy, documenting relative proportions of C_3 and C_4 vegetation by isotopic analyses is a useful tool in paleoenvironmental reconstructions. Specifically, the link between C_4 metabolism and grasses provides a means of identifying grass-dominated plant communities such as open woodlands, savannas, and grasslands. However, the large variety of C_3 -dominated habitats, ranging from lowland rainforest to arid bushland to cold-climate grassland, limits the resolving power of a C_3 isotopic signal in reconstructing vegetation. In addition, in adopting a uniform approach, modern ecosystems typically provide the template for interpreting isotopic records of the past. Past habitats may in fact have no modern analogues. An isotopic signal indicating a mixture of C_3 and C_4 species could represent tropical savanna with a significant woody component, a cool temperate prairie with a mixture of C_3 and C_4 grasses, or a tropical grassland with no modern analogue having a mixture of C_3 and C_4 grasses. The possibility of C_3 grass-dominated ecosystems at latitudes dominated by C_4 grasses today may complicate interpretations of past landscapes.

Assuming that CAM plants comprised an insignificant portion of the biomass, the key to using metabolic pathways to interpret paleoenvironment is in retrieving an intact isotopic record reflecting the relative proportion of vegetation using C_3 versus C_4 photosynthetic pathways in the past. There are a number of approaches, including isotopic analyses of: (1) preserved organic plant matter in paleosols (Ambrose & Sikes, 1991; Kingston et al., 1994); (2) organic material within opal phytoliths (Kelly et al., 1991, 1993; Fredlund & Tieszen, 1994, 1997); (3) paleosol carbonates, which formed in equilibrium with local paleovegetation and provide an average isotopic signature of plant biomass during the interval in which the paleosol formed (Cerling & Hay, 1986; Amundson & Lund, 1987; Quade et al., 1989b; Kingston et al., 1994; Sikes, 1994, 1996); (4) carbonate occluded in fossil bone, enamel, or eggshells, which reflects available dietary plants (Lee-Thorp & van der Merwe, 1987; Quade et al., 1992; Morgan et al., 1994; Stern et al., 1994; Cerling et al., 1997b; Johnson et al., 1997); and (5) terrestrial organic carbon in marine

sediments (France-Lanord & Derry, 1994; Bird et al., 1995; Gouli et al., 1997). Of these techniques, analyses of fossil herbivore enamel and paleosol components have been most widely applied and are most relevant to the discussion of the origin of grass-dominated ecosystems.

Theoretical models and studies of modern soils have established a correlation between the stable carbon isotopic composition of soil components and prevailing climatic and ecological conditions (Cerling, 1984; Amundson et al., 1989; Quade et al., 1989b). In general, where plant respiration is high, the carbon isotopic composition of soil CO₂, and soil carbonate equilibrating with soil CO₂, are controlled by the proportion of surface vegetation utilizing the C₃ versus C₄ photosynthetic pathway. As soils usually form over hundreds or even thousands of years, they preserve a paleoenvironmental record averaged over an interval spanning many generations of plants.

Soil carbonates typically form in semiarid to sub-humid climates (rainfall normally less than 75–85 cm/yr.) at some depth below surface. Pedogenic carbonate generally precipitates in relatively dry soils where net evaporation exceeds precipitation, conditions that are typically associated with grass or mixed grass and shrub-dominated ecosystems. Buried paleosols with associated soil carbonates and organic matter can retain the biogenic isotopic signal of the original soil system. Although soil carbonate nodules can be reworked, where preserved, they are generally not subjected to the taphonomic and sampling filters that can seriously bias representation of the faunal and floral records. Ecosystems commonly associated with surfaces subjected to erosion, such as alluvial fans, may be underrepresented in paleosol studies. Non-calcareous paleosols may be indicative of environmental conditions that inhibit formation or preservation of pedogenic carbonate nodules (e.g., forested habitats with acidic soils, heavy precipitation that leaches carbonates from soil profiles, or lack of Ca in the parent material).

Analysis of the isotopic signature in fossil enamel corroborates analyses of paleosol components documenting relative proportions of C₃ and C₄ vegetation in the past. The carbon isotopic composition of modern herbivore tissue, including tooth enamel, is directly related to the ingested $\delta^{13}\text{C}$ value of the primary photosynthesizing plants in the food chain (DeNiro & Epstein, 1978; Tieszen et al., 1983; Ambrose & DeNiro, 1986). The relationship between the carbon isotopic composition of body tissue and diet was initially exploited primarily to address archaeological issues such as the introduction of

maize, a C₄ domesticate, into previously C₃-dominated New World agricultural economies (Vogel & van der Merwe, 1977; van der Merwe & Vogel, 1978). Within the last decade, this approach has been extended to fossil assemblages in which the focus of isotopic analysis has shifted from bone collagen and minerals to enamel apatite. Application of isotopic analyses to fossil enamel strictly for paleodietary studies has been limited (e.g., Ericson et al., 1981; Lee-Thorp et al., 1989), and instead its use has been primarily for paleoecological reconstruction (Thackeray et al., 1990; Kingston, 1992; Quade et al., 1992; Wang et al., 1993; Morgan et al., 1994; Quade et al., 1994; Cerling et al., 1997b).

Reconstructions of past habitats based on isotopic analysis of fossil enamel must be carefully interpreted as the paleoenvironment has not been sampled directly but rather through a dietary filter. Specific aspects of feeding behavior are dictated not only by available food items but also by selectivity, competitive exclusion, and migration. Modern giraffes, for example, typically inhabit open biomes dominated by C₄ grasses yet their enamel yields a C₃ isotopic signature. Modern ruminant herbivore species have traditionally been placed in three broad dietary categories: browsers, grazers, and mixed-feeders conveniently associated with C₃, C₄, and mixed C₃/C₄ isotopic signals, respectively. This set of categories is based on the assumption that all available grass is C₄, an unrealistic presumption in the past, or in the present in areas where C₄ plants do not grow (Morgan et al., 1994; MacFadden, 1997).

NORTH AMERICA

SUMMARY

The largest continuous grasslands of North America, the Great Plains, are bounded to the west by the Rocky Mountains, to the east by deciduous or coniferous forest, to the north by coniferous forest, and to the south by the Gulf of Mexico (Fig. 1). More restricted grassland areas include the California prairies, the Palouse prairie of the northwestern U.S. and southern British Columbia, and the desert grasslands of the Sonoran and Chihuahuan deserts in the southwestern U.S. and Mexico (Coupland, 1992b).

The oldest record of grasses in North America is a macrofloral assemblage from the early Eocene of Tennessee (Crepet & Feldman, 1991; Crepet & Herendeen, 1992), but grass pollen and macrofossils are rare throughout the Eocene and Oligocene (Fig. 2). In the early Miocene of the Great Plains

North America

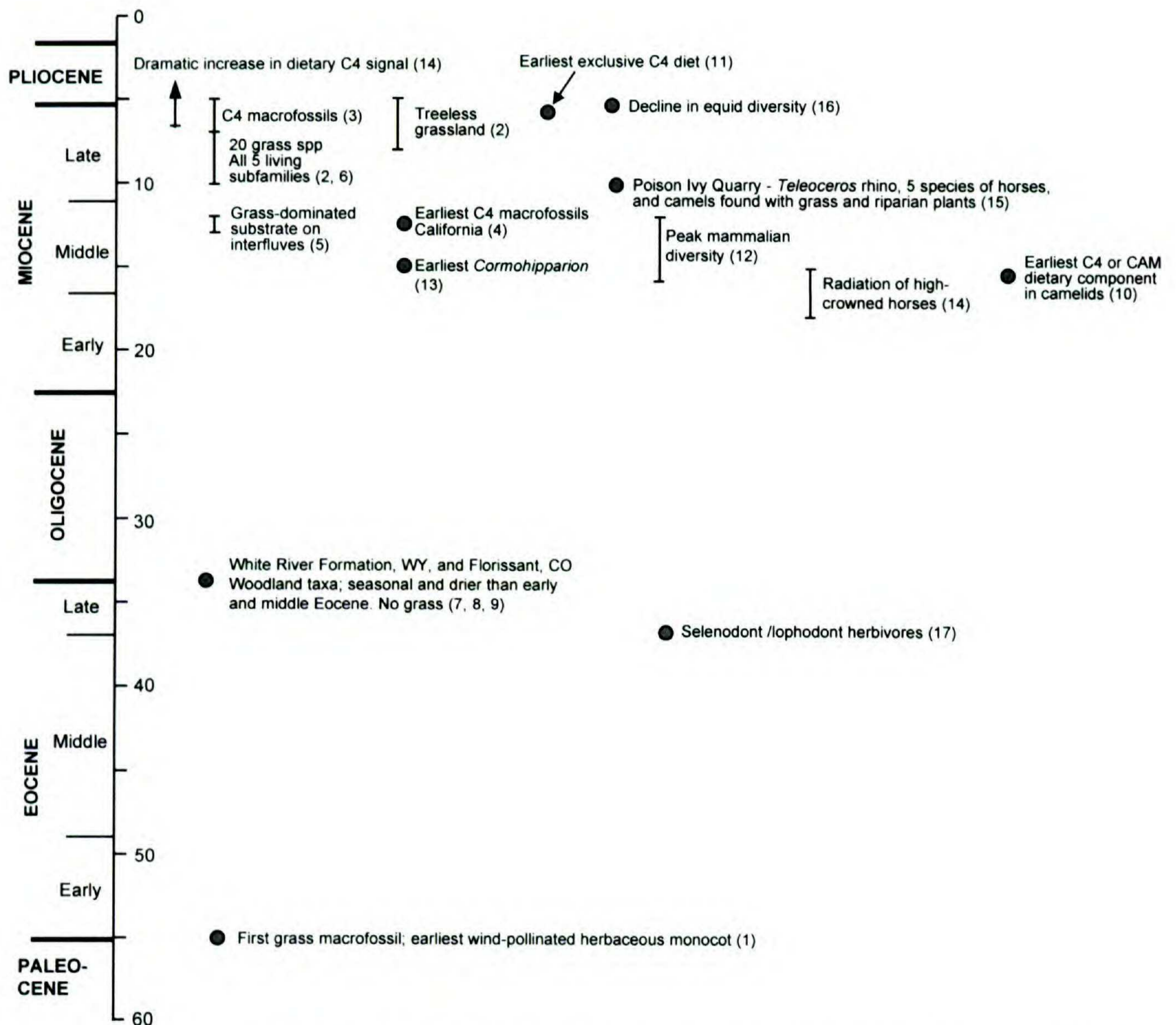


Figure 2. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in North America. Solid lines denote the presence of fossil data throughout the time interval shown. Dots indicate data from specific, well-constrained times. Sources: (1) Crepet & Feldman (1991), (2) Thomasson (1990), (3) Thomasson et al. (1986), (4) Nambudiri et al. (1978), (5) MacGinitie (1962), (6) Thomasson et al. (1990), (7) MacGinitie (1953), (8) Leopold & MacGinitie (1972), (9) Leopold et al. (1992), (10) La torre et al. (1997), (11) Cerling et al. (1997b), (12) Webb & Opdyke (1995), (13) Bernor et al. (1996a), (14) MacFadden & Hulbert (1988), (15) Voorhies & Thomasson (1979), (16) MacFadden & Cerling (1994), (17) Jernvall et al. (1996).

region, only one grass species is recognized based on macrofossils (Elias, 1942). Macrofloras document the emergence of grass-dominated environments between 13 and 10 Ma (MacGinitie, 1962; Thomasson, 1990). Relatively treeless grasslands may have been present by 8 Ma (Thomasson, 1990; see also Axelrod, 1985). By 7 Ma grass diversity includes all five living subfamilies (Thomasson, 1990). Leaf anatomical evidence for C_4 photosynthesis is documented by 12.5 Ma (Nambudiri et al., 1978; Whistler & Burbank, 1992).

The adaptive radiation of grazing horses occurs in the Miocene (18 to 15 Ma; MacFadden & Hulbert, 1988). The ungulate community as a whole is diverse in the Miocene; however, from 12 Ma until the end of the Miocene, diversity declines, especially among larger, more specialized browsing forms. After 5 Ma, grazing horse diversity drops precipitously.

The earliest potential evidence for a C_4 dietary component is from 15.6 Ma (Latorre et al., 1997). Mixed C_3/C_4 diets are clearly evident by 7 Ma

(MacFadden & Cerling, 1996), and by 6.8 Ma there appears to be a dramatic increase in the dietary C_4 component of horses in the southern portion of North America (Cerling et al., 1997b). Earliest reports of enamel isotopic values consistent with a pure C_4 diet are at 5.7 Ma from sites in Mexico (Cerling et al., 1997b). The transition from C_3 to predominately C_4 dietary signatures suggests that up until that time the contribution of grass in the ecosystem to diet was mainly from C_3 species. More northerly sites document the presence of C_4 grasses around 4 Ma. However, isotopes do not at any time suggest exclusive reliance on C_4 grasses by equids above 37°N. The extent to which C_4 grasses expand into North American biomes appears to be a function of latitude.

PALEOBOTANY

The earliest known record of Poaceae in North America consists of entire plants, spikelets, and inflorescence fragments from the early Eocene Claiborne Formation of Tennessee (Crepet & Feldman, 1991; Crepet & Herendeen, 1992). However, grass macrofossils and pollen are rare or absent in the other Paleogene deposits where forest or woodland vegetation was prevalent (Dilcher, 1973; Hickey, 1977; Wolfe, 1977; Graham, 1993; Manchester, 1994; Wing et al., 1995; Wing, 1998, and references therein).

Seasonal climates appear by the middle Eocene in western North America and along the Gulf Coast based on pollen and plant macrofossils (Dilcher, 1973; Frederiksen, 1991; Wolfe, 1994; Wing, 1998). However, only 8 of 56 Gulf Coast middle Eocene to early Oligocene pollen assemblages contain (infrequent) grass pollen, indicating the lack of grass dominance even in possible marsh settings (Frederiksen, 1981). In the Rocky Mountain region, the Florissant flora of Colorado (\approx 34 Ma), containing woody xerophytes and riparian taxa, represents open evergreen oak and pine woodlands on slopes leading to riparian settings (MacGinitie, 1953; Leopold et al., 1992). A fossil grass from Florissant, *Stipa florissantii* Knowlton, is not interpreted as indicating a grassland environment (MacGinitie, 1953). Pollen assemblages from Florissant and other middle to late Eocene localities indicate that grasses were absent in woodland understories (Leopold & MacGinitie, 1972; Leopold et al., 1992). A single silicified grass caryopsis (grain with enclosing palea and lemma) is reported from the Cedar Creek Member of the White River Formation, Colorado (\approx 33 Ma, Emry & Russell, 1987; Woodburne & Swisher, 1995), but additional

specimens have not been found despite a decade of continued searching (Galbreath, 1974). Pollen samples from the Poison Spring locality in the White River Formation, Wyoming, yielded a pollen assemblage similar to that at Florissant, with which it is approximately equivalent in age. No grass pollen was found in the assemblage (Leopold & MacGinitie, 1972; Leopold et al., 1992). The paleofloral data contradict interpretations based on paleosols indicating wooded grasslands by 34 Ma and open treeless grassland on interfluves by the middle Oligocene (Retallack, 1992; for a discussion of paleoenvironmental interpretations based on soil classification, see Dahms et al., 1998; Retallack, 1998; Dahms & Holliday, 1998).

The Kilgore flora (Cherry County, Nebraska, MacGinitie, 1962) occurs in the Crookston Bridge Member of the Valentine Formation (Skinner & Johnson, 1984), which has yielded mammals indicative of the Barstovian Land Mammal Age (12–13 Ma, Tedford et al., 1987). Most woody taxa assigned to extant genera are riparian (e.g., *Juglans* L., *Fraxinus* L., *Carya* Nutt., *Nyssa* L., *Acer* L., and *Alnus* Mill.). Others such as *Quercus* L. and *Pinus* L. prefer drier substrates. These taxa are interpreted as forming a mixed open chaparral on interfluves, with grasses dominating the open areas (MacGinitie, 1962: 84). The pollen flora supplements macrofossil assemblages by providing a record of herbaceous families, such as Poaceae, Chenopodiaceae, Compositae, and Cyperaceae; however, relative pollen percentages are not published (MacGinitie, 1962).

The earliest C_4 grass macrofossil, *Thomlinsonia thomassonii* Tidwell & Nambudiri (1989), is from the Dove Spring Formation in the Ricardo Group of California (Nambudiri et al., 1978) now dated to approximately 12.5 Ma (Whistler & Burbank, 1992). Roots, culms, and leaves, including Kranz anatomy in leaf cross section, are preserved and are characteristic of C_4 grasses. Stable carbon isotope values from the fossils confirm the plants were C_4 photosynthesizers (Nambudiri et al., 1978). However, carbon isotope values for equid tooth enamel from the same locality indicate that the majority of equid diet consisted of C_3 vegetation (Cerling et al., 1998). Fossil wood from this locality is comprised most commonly of *Robinia* L. and a palm, with *Quercus*, *Cupressus* L., and *Pinus* species less common (Webber, 1933). The paleoenvironment reconstructed by Webber (1933) is similar to the grassy woodlands in the lower uplands of the modern Sonoran Desert region, but the amount of grass cover relative to wooded area is indeterminate from the data.

The Miocene record of macrofossils from the Great Plains of North America is unique for the Tertiary in providing information about phylogenetic relationships, species richness, and paleoecology of grasses (Elias, 1942; Thomasson, 1978, 1979, 1987, 1990). Grass taxa are documented by silicified or calcified reproductive parts (e.g., Elias, 1932, 1942; Thomasson, 1979, 1985; Gabel et al., 1998) and leaves preserving micromorphology and internal anatomy (Thomasson, 1984). Only one species is known from the early Miocene, but there appears to be continuous diversification from the early to middle Miocene (Elias, 1942). Between 10 and 7 Ma, Thomasson (1990) reported at least 20 species representing the five extant grass subfamilies. Grass fossils from the Great Plains are found in the same lithologic units that produce dated vertebrate assemblages, permitting age assignments for paleofloras based on vertebrate biochronology (Thomasson, 1990; Woodburne & Swisher, 1995).

The Poison Ivy flora from the Ash Hollow Formation (\approx 10 Ma, Antelope County, Nebraska, Thomasson, 1990) overlies the Valentine Formation, and occurs in an ashfall containing a late Clarendonian mammal fauna (see below). The flora includes hackberry, walnut or hickory, forbs, sedges, horsetails, and three grass taxa dominated by fossil species *Berriochloa communis* Thomasson (= *Stipidium commune* Elias). The early Hemphillian Russ's flora (between 8.5 and 7 Ma, Garden County, Nebraska, Thomasson, 1990) contains 10 grass species among four of the five living subfamilies. Extant species of the genus *Panicum* L. (subfamily Panicoideae) that occur at Russ's flora exhibit both C₃ and C₄ photosynthesis. A leaf fragment from Russ's flora is in the subfamily Arundinoideae, which includes both C₃ and C₄ extant genera. The Minium Quarry (approximately 7 Ma, Graham County, Kansas, Thomasson et al., 1990) has a diverse grass assemblage including 12 species among all 5 living subfamilies, and a C₄ fossil identified by Kranz anatomy in leaf cross section (Thomasson et al., 1986). Although scattered trees were present at the Russ's and Poison Ivy sites, Thomasson (1990) reported that grassland was most likely the dominant community at all localities.

Other significant Miocene paleofloras include the Beaver County floras of western Oklahoma (late Clarendonian, \approx 10 Ma), and the Logan County, Kansas, flora (Berry, 1918; Chaney & Elias, 1936). These are lacustrine deposits preserving aquatic and riparian taxa, approximately equivalent in age to the grass and forb assemblages of Elias (1942, and discussed in Chaney & Elias, 1936). Both are interpreted as representing a prairie environment

with primarily riparian trees preserved. The Logan County flora represents a drier environment than the Beaver County assemblages based on species composition and smaller size of leaves.

Thomasson (1990) interpreted the rich middle to late Miocene fossil grass record of the central and northern Great Plains as a grass-dominated landscape with scattered trees, at least by 10 to 11 Ma, and a treeless grassland by 5 to 8 Ma. Chaney and Elias (1936) assumed that grassy interfluves of 10 to 11 Ma were much like the treeless prairie of today. Axelrod (1985), in contrast, reconstructed woodlands and forests for the interfluves with park-like grassy openings until 7 to 5 Ma, by which time grasses had become dominant on the landscape. More recent analyses of Ogallala Group macrofossils from South Dakota and northern Nebraska support the contention that by the middle Miocene grass-dominated environments were present throughout the northern and southern Great Plains (Gabel et al., 1998).

Paleogene and early Miocene floras from the Pacific Northwest record widespread forests as far east as the modern Columbia Plateau (Chaney, 1959; Manchester, 1987, 1994). A precipitous cooling is evident in leaf assemblages from western North America near the Eocene-Oligocene boundary (Wolfe, 1994). Increasing aridity or continentality is indicated by the middle Miocene (Barnosky, 1984; Wolfe, 1994). Pollen from the late Barstovian (\approx 13 Ma) Succor Creek Formation indicates local grass-dominated parklands in early successional communities on volcanic ash (Taggart & Cross, 1990). By 10 Ma, forests gave way to a more open landscape in response to a rainshadow created by uplift of the Cascade Range (Clements & Chaney, 1937), but grass-dominated vegetation was probably uncommon until the middle to late Pliocene (Leopold & Denton, 1987).

PALEOFAUNA

The most recent review of the North American mammalian fauna is provided by Webb and Opdyke (1995; see also Webb, 1977, 1983a, b, 1984, 1989; Krause & Maas, 1990; Stucky, 1990; Janis, 1993; Janis et al., 1998; Woodburne & Swisher, 1995). The Cenozoic Era, as recorded in terrestrial rocks in North America, is divided on the basis of fossil mammals into 19 Land Mammal Ages (LMAs) to refine chronological resolution. In addition, Tertiary vertebrate assemblages can be grouped into six ecologically significant chronofaunas that remain relatively stable in composition and diversity throughout their duration, yet within which minor

change can be demonstrated. These chronofaunas are bounded primarily by periods of immigration accompanied by extinction, which dramatically change the character of succeeding chronofaunas, but their boundaries do not necessarily coincide with those of LMAs. Each chronofauna exhibits distinct ecological attributes, providing clear indications, based on mammals, of the environmental history of North America.

As summarized by Webb and Opdyke (1995), the Tertiary began with a Paleocene Chronofauna comprised at the ordinal level primarily of Late Cretaceous holdovers. Arboreal adaptations were common. Most species were small to medium-sized, although there is a general increase in size and diversity of herbivores through the Paleocene, including the precociously hypsodont taeniodonts, the horned, browsing dinoceratans, and pantodonts, all three immigrants from Asia. During the Clarkforkian and Wasatchian (56.5–50 Ma) land mammal ages, waves of immigrants changed the character of the North American fauna, giving rise to the Eocene Chronofauna. Rodents, coryphodonts, and tilodonts entered from Asia. Strong similarities exist between the North American and European faunas of the early Eocene, reflecting a North Atlantic immigration route (Thulean Bridge). Perissodactyls and artiodactyls appear for the first time in North America. Low-crowned perissodactyls and rodents diversify greatly. Arboreal mammals, including primates, are most abundant during the middle Eocene. Forest-dwelling primates are found within the Arctic Circle on Ellesmere Island (West & Dawson, 1978).

Selenodont, or crescent-shaped, tooth cusps are characteristic of the early Eocene (Wastachian) genus *Meniscotherium* Cope. Special environmental significance was previously accorded *Meniscotherium* based on its selenodont teeth and perceived distribution across North America. A more recent analysis based on dental microwear indicates food with a high grit content without significance for a diet or environment predominated by grass (Williamson & Lucas, 1992).

By the middle Eocene seasonal aridity is suggested by evaporite and oxidized redbed deposits associated with Green River lakes (Bradley, 1947). The Uintan rodent *Protoptychus* Scott (44–45 Ma) from Wyoming has inflated bullae; its elongate hindlimbs, short forelimbs, and other skeletal features are indicative of ricochet locomotion (Wahlert, 1973; Brown & Yalden, 1973; Turnbull, 1991). *Protoptychus* strongly resembles kangaroo rats and jerboas in its adaptations, both of which are characteristic of arid, open regions, thus suggesting to

Turnbull (1991) that in the area of the Uinta and Washakie basins, riverine subtropical forests were separated by arid divides between the alluvial drainages.

The Eocene Chronofauna drew to a close at approximately 40 Ma (late Eocene), culminating in the Duchesnean LMA. New waves of immigration introduced the White River Chronofauna. The number of herbivorous species, including browsers, especially selenodont species, increased. New to this chronofauna were camels, peccaries, oreodonts, and rhinoceroses. Among the smaller mammals, shrews, squirrels, beavers, pocket mice and some other rodent families, and rabbits were new. For the first time in North America, hypsodont mammals, both larger and smaller, were diverse. Some of the ungulates [e.g., *Leptomeryx* (Leidy)] are interpreted to have behaved similarly to gazelles, as herbivores that ate green grass in the growing season but subsisted on browse during the dry season (Janis, 1982). None of the White River herbivores appears to have been a strict grazer. Burrowing species indicative of well-drained soils increased, and arboreal species decreased. Aquatic reptile diversity declined (Hutchison, 1992). The early Miocene Runningwater Chronofauna, followed by the Sheep Creek Chronofauna, are characterized by immigrations and relatively diverse faunas indicative of mixed, but progressively more open habitats.

The Clarendonian Chronofauna, beginning about 18 Ma in the Hemingfordian LMA, spans the Barstovian, Clarendonian, and Hemphillian land mammal ages, which end about 5 Ma. Between 18 and 15 million years ago, during the inception of the Clarendonian Chronofauna, horses appear to include greater amounts of graze in their diets. Beginning with *Merychippus* Leidy, high-crowned horses rapidly radiated and diversified (MacFadden & Hulbert, 1988; MacFadden et al., 1991; Hulbert & MacFadden, 1991; Hulbert, 1993), presumably signifying the increasing prevalence of grass in their diets and in the environment (Webb, 1983a; Hayek et al., 1992). This rich chronofauna exhibits its highest levels of mammalian diversity in the Barstovian, between about 16 and 12 Ma (141 species in 60 genera in 16 families).

Voorhies (1990) listed 28 ungulate species from the Barstovian Norden Bridge Quarry, Nebraska. Grazing horse diversity reached 16 contemporaneous species. The large rhinoceroses *Teleoceras* Hatcher and *Aphelops* Cope, the proboscideans *Miomastodon* Osborn and *Gomphotherium* Burmeister, and other taxa dispersed from Asia into North America early in this interval. Beginning about 12

Ma, ungulates began a decline in diversity from their Barstovian peak.

The three-toed hipparionine horse genus *Cormohipparion* Skinner & MacFadden first appears at approximately 15 Ma (Barstovian) and is widely distributed in North America until about 8 Ma. *Cormohipparion* is important because closely related equids dispersed throughout Eurasia subsequent to the first record of *Cormohipparion* in North America. This hipparionine dispersal (see discussion of the Eurasian paleofauna below) has been interpreted as representing the spread of grass-dominated ecosystems in the Old World during the Miocene, although the pattern may actually be more complex ecologically. The New World origin of the Old World hipparionine radiation can be narrowed to a subset of species that has been suggested to be within the *Cormohipparion occidentale* Leidy group (Bernor et al., 1996c; Woodburne, 1996), whose earliest record is 12.7 Ma (late Barstovian), and which lasted until slightly younger than 10 Ma (late Clarendonian or early Hemphillian; Woodburne & Swisher, 1995).

Cormohipparion occidentale occurs in the Clarendonian Dove Spring Formation, California, along with a diverse suite of mammals, including five other species of horses (Whistler & Burbank, 1992). As seen above in the discussion of North American paleobotany, the Dove Spring flora includes grass blades with Kranz anatomy, documenting the presence of C_4 grass at 12.5 Ma, yet isotopic values for tooth enamel of *Cormohipparion occidentale* and *Pliohippus tantalus* Merriam indicate that C_4 plants were insignificant components in the diets of those horses (Cerling et al., 1998).

The Poison Ivy Quarry (\approx 10 Ma, Clarendonian) in Antelope County, Nebraska, is particularly significant with respect to the origin of grass-dominated ecosystems because the vertebrate assemblage is associated with paleobotanical remains in a volcanic ash (see above). Remains of the barrel-shaped rhinoceros *Teleoceros major* Hatcher were found with grass remnants in the oral cavity and rib cage, demonstrating that this hypsodont rhinoceros ate grass (Voorhies & Thomasson, 1979; see also MacFadden, 1998). Other taxa at the site include five species of horses and several camels. The vegetation was mixed, including riparian woody species and a significant grass component, consistent with the mammalian assemblage.

The diversity of mammals in the early part of the Clarendonian Chronofauna presumably reflects a rich mosaic of environments accommodating the spectrum of feeding adaptations that had been evolving throughout the Cenozoic. As one correlate

of this diversity, elements of the Barstovian fauna were able to take advantage of grassy parkland successional habitats created by volcanic activity as demonstrated in the Succor Creek Formation, Oregon (Taggart & Cross, 1990). By the end of the Hemphillian (5 Ma), generic diversity was reduced to half that of the Barstovian near the beginning of the chronofauna (Webb & Opdyke, 1995). Browsers were initially affected more than grazers. Webb and Opdyke (1995) suggested that this pattern indicates the development of an extensive grassland. The inferred increase in grass cover coincided with a reduction in ungulate diversity. Between about 7 and 5 million years ago, equid diversity in North America precipitously declined, only hipparionines and *Equus* L. remaining into the Pliocene (MacFadden & Hulbert, 1988). Accompanying these changes in the Hemphillian was an increase in faunal provincialism, an introduction of immigrants, and an increase in rodents with high-crowned teeth (Hulbert, 1987; Jacobs, 1977; MacFadden et al., 1979; Shottwell, 1958, 1961; Tedford & Gustafson, 1974; Webb, 1989). Stable carbon isotopes (see below) indicate a dramatic dietary shift from C_3 to C_4 plants in the late Miocene, during the interval when ungulate diversity was decreasing (Cerling et al., 1998).

The ungulate component of the Clarendonian Chronofauna was convergently similar to the modern African savanna fauna (Hulbert, 1982; Webb, 1983a; Janis, 1984). However, toward the end of the Miocene in North America, unlike modern Africa, the fauna was deficient in hypsodont bovids, having instead a variety of horses, and lacked the diversity of small, lower-crowned browsing ungulates (Janis, 1984, 1995).

STABLE ISOTOPES

Initial investigations of equid enamel collected from western North American fossil localities indicated that C_4 grasses became an important dietary component starting between 7 and 6 Ma (Cerling et al., 1993). This dietary shift, in conjunction with isotopic data from Pakistan (Quade et al., 1989a, 1992), was interpreted to reflect a rapid global expansion of C_4 -dominated biomes attributed to global changes in both the carbon budget and the meteoric water cycle, rather than reflecting only regional climatic change. Specifically, this expansion was linked to decreasing atmospheric pCO_2 levels that would favor C_4 grasses over C_3 vegetation. Cerling et al. (1993) observed that the late Miocene $\delta^{13}C$ shift in equid enamel from North America did not correspond to the early to middle

Miocene development of hypsodonty and suggested a revision in the interpretation of the relationship of high-crowned teeth to the spread of grass-dominated environments.

Subsequent studies of fossil herbivore enamel (MacFadden & Cerling, 1994, 1996; Wang et al., 1994; Cerling et al., 1997b, 1998; Latorre et al., 1997) provide additional support for C_4 biomass expansion in the late Miocene. Based on isotopic analyses of 50 fossil horse enamel samples from various localities throughout North America up to 52 Ma, Wang et al. (1994) noted that the first strongly enriched $\delta^{13}C$ values in tooth enamel, indicating a significant to exclusive C_4 dietary component, occurred between 7 and 5 Ma. They pointed out that the early to middle Miocene equid diversity climax and development of hypsodonty cannot be linked to the expansion of strictly modern savanna ecosystems, which contain significant proportions of C_4 biomass. However, they suggested that C_3 grasslands and savannas could have existed under atmospheric pCO_2 levels higher than today (Wang et al., 1994).

The carbon isotopic signature of fossil enamel from equids, gomphothere proboscideans, and camelids from the late Miocene to Pliocene of New Mexico and Arizona indicates that C_3 plants dominated diets there until 6.3 Ma (Latorre et al., 1997). However, the isotopic values for camelid enamel as old as 15.6 Ma are interpreted as indicating a minor C_4 or CAM dietary component. After 6.3 Ma there is a dramatic increase in C_4 vegetation in the diet of the fossil horses. During this transition, the isotopic signal of camelid and gomphothere enamel indicates only moderate shifts toward an increase in the dietary C_4 component.

Dividing isotopic data on equid enamel from North America into a high-latitude group ($> 37^\circ N$) and a low-latitude group ($< 37^\circ N$), Cerling et al. (1997b) noted a significant dietary shift in low-latitude equids during the late Hemphillian. Sites older than 7 Ma have $\delta^{13}C$ values consistent with a C_3 -dominated diet, but by 6.8 Ma a significant C_4 component is evident and by 5.7 Ma exclusive C_4 diets are indicated. Equid enamel analyzed from the high-latitude group do not indicate a C_4 dietary component until about 4 Ma, and northern horses consumed a smaller fraction of C_4 biomass than their southern counterparts. The variability in C_4 dietary component noted in North America and at intermediate latitudes ($25\text{--}40^\circ N$ and S) elsewhere in the world potentially reflects the variability of growing seasons in different regions, variability in the amount of C_4 biomass during different parts of the growing season, or greater sensitivity at higher

latitudes to climatic fluctuations (Cerling et al., 1997b).

Analyses of the enamel of fossil mammalian herbivores comprising the orders Proboscidea, Perissodactyla, and Artiodactyla from 17 fossil localities in Florida ranging in age from 9.5 to 0.1 Ma indicate an isotopic shift toward a C_4 diet starting at 7.0 Ma (MacFadden & Cerling, 1996). Prior to 7 Ma, the carbon isotopic values of all tooth samples are consistent with a diet comprised only of C_3 plants. At about 7 Ma, the $\delta^{13}C$ values of fossil enamel indicate both C_3 and mixed C_3/C_4 diets, presumably reflecting the spread of C_4 -based plant communities in this region of North America. By the latest Hemphillian (about 5 Ma) there is evidence for pure C_4 grass diets, although there is a gap in the fossil record between 5 and 7 Ma and exclusive C_4 diets may have occurred earlier. MacFadden and Cerling (1996) noted that the mixed dietary signals from teeth of *Cormohipparion* in the latest Hemphillian could reflect either a mixed diet of C_4 grass and C_3 browse or a diet of a mixture of C_3 and C_4 grasses.

One of the more interesting features of the isotopic record of North America is the significant time difference between the middle Miocene radiation of equids, usually interpreted as reflecting adaptations to grazing, and the spread of C_4 vegetation in the late Miocene. These data suggest that either C_3 grasses comprised a significant proportion of the vegetation during the middle Miocene and probably dominated communities in some regions, or that early high-crowned horses were not obligate grazers. The roughly contemporaneous spread of C_4 -dominated biomes and a precipitous decline in equid diversity as well as other faunal groups is also interesting. An increase in dietary C_4 grasses reflects an expansion of C_4 grasslands that would traditionally be expected to favor a grazing fauna. MacFadden and Cerling (1994) suggested the late Miocene isotopic shift may have involved the replacement of savanna and forest biomes with lower-productivity C_4 grasslands.

EURASIA

SUMMARY

Eurasia exhibits a great deal of regional provincialism as might be expected from the longitudinal and latitudinal extent of the landmass and the significant tectonic processes that have affected it throughout the Tertiary, including such events as the retreat of the Turgai Straits, the collision of India with Asia, the closure of the Tethys, the Alpine Orogeny, and the desiccation of the Mediterranean

Basin. This large region includes the temperate grasslands of easternmost Europe, the Ukraine, Russia, and interior northern China, as well as the tropical and subtropical savanna regions of Asia and the Indian subcontinent. The natural vegetation of most of Europe is forest today and has been throughout the Tertiary (Fig. 1).

Graminidites pollen and probable grass macrofossils occur in the early Eocene London Clay flora, England (Chandler, 1964; Thomasson, 1987; Boulter, 1988). Nevertheless, the Tertiary paleobotanical record of western Europe documents the widespread presence of forest communities (Fig. 3). A period of drying and cooling begins in the late Eocene. Species richness declines into the Oligocene, and evergreen tropical and subtropical species are replaced by deciduous taxa and conifers. This trend continues throughout the Tertiary, progressing from north to south. Pollen evidence indicates the initial spread of grassland and steppe communities in the region around the Black Sea beginning in the late Miocene. However, grass pollen is not abundant in Europe until the middle Pliocene (Traverse, 1982; Benda, 1971).

Pollen records from the northern interior of China indicate open environments in the Oligocene, but significant grass cover is absent until the early Miocene (Leopold et al., 1992). Rare *Graminidites* pollen is present in the early Tertiary Subathu Formation of northwestern India (Mathur, 1984; Singh & Sarkar, 1990), along with palynological evidence of coastal, semi-evergreen tropical conditions. Early Miocene plant macrofossils from the Siwalik section of northwestern India indicate forest environments, although pollen samples from the same region contain 8% grass pollen. An increase in abundance of grass pollen occurs in the late Miocene, documenting the development of a grass-dominated ecosystem (Mathur, 1984). In Nepal, late Miocene macrofossils indicate deciduous forest, but after the late Miocene grasses are represented by pollen and a few macrofossils (Awasthi & Prasad, 1990; Sarkar, 1990; Prasad & Awasthi, 1996).

The vertebrate record of central Asia is consistent with open habitat beginning in the Oligocene. Throughout the Neogene, the fauna of western Europe indicates closed habitats, as compared to more open habitats to the east. Hipparionine horses originated in North America, but dispersed across Eurasia between 10.9 and 10.7 Ma, with an Old World radiation of browsing, mixed-feeding, and grazing species. The late Miocene fauna of Greece (8.3–7 Ma) is characterized by a diverse suite of some 30 species of mainly mixed-feeding and browsing ungulates with few grazers. Between 9 and 7 Ma, sig-

nificant faunal changes occur in the Siwalik sequence of Pakistan, including the presence of hypsodont bovids, porcupines, and rabbits, and the disappearance of large hominoids, which indicate the opening of habitats.

Isotopic studies of paleosol components and fossil herbivore enamel from Europe do not indicate significant C₄ biomass at any time during the Neogene. The isotopic record of Europe throughout the Miocene indicates a predominance of C₃ vegetation. In Asia, on the other hand, C₄ plants are isotopically recorded as a minor dietary component at 9.4 Ma in the Siwalik sequence of Pakistan, increasing gradually as a foraging resource until exclusively C₄ diets are documented about 5 Ma (Morgan et al., 1994; Cerling et al., 1997b). Analyses of paleosol carbonates from Pakistan and Nepal (Quade et al., 1989a, 1995a) and organic matter from the Bengal Fan (France-Lanord & Derry, 1994) indicate a more abrupt shift from C₃- to C₄-dominated vegetation between 8.1 and 6.5 Ma.

PALEOBOTANY

Europe. The European Tertiary paleobotanical record primarily documents a history of changing forest composition. Grass leaf and inflorescence fragments are reported from the early Eocene London Clay flora (Chandler, 1964; Thomasson, 1987). A palynological survey of aquatic monocotyledons from the Tertiary of southern England and northern France includes the occurrence of *Graminidites* pollen beginning in the early Eocene with the London Clay (Boulter, 1988), but these have not been evaluated to determine the absence of scrobiculae or presence of microchannels. Moreover, Wilkinson and Boulter (1980: 46) reported that Oligocene samples from England have up to 3% *Graminidites* having a poorly defined pore without a distinct annulus, thus implying these pollen are probably not Poaceae.

Late Eocene to Oligocene paleobotanical records from western and central Europe indicate a general increase in seasonality, cooling, and drying (Collinson, 1992). Plant communities show an increasing dominance of deciduous and coniferous taxa accompanied by an overall decrease in species richness and the occurrence of arid-adapted taxa such as *Ephedra* L., and *Acacia* Mill. (Collinson, 1992, and many references therein; Cavagnetto & Anadon, 1996). An extensive herbaceous component is lacking in most Paleogene non-aquatic communities; however, pollen of herbaceous plants, including grass, occurs in the early Oligocene of north-eastern Spain (Cavagnetto & Anadon, 1996).

Eurasia

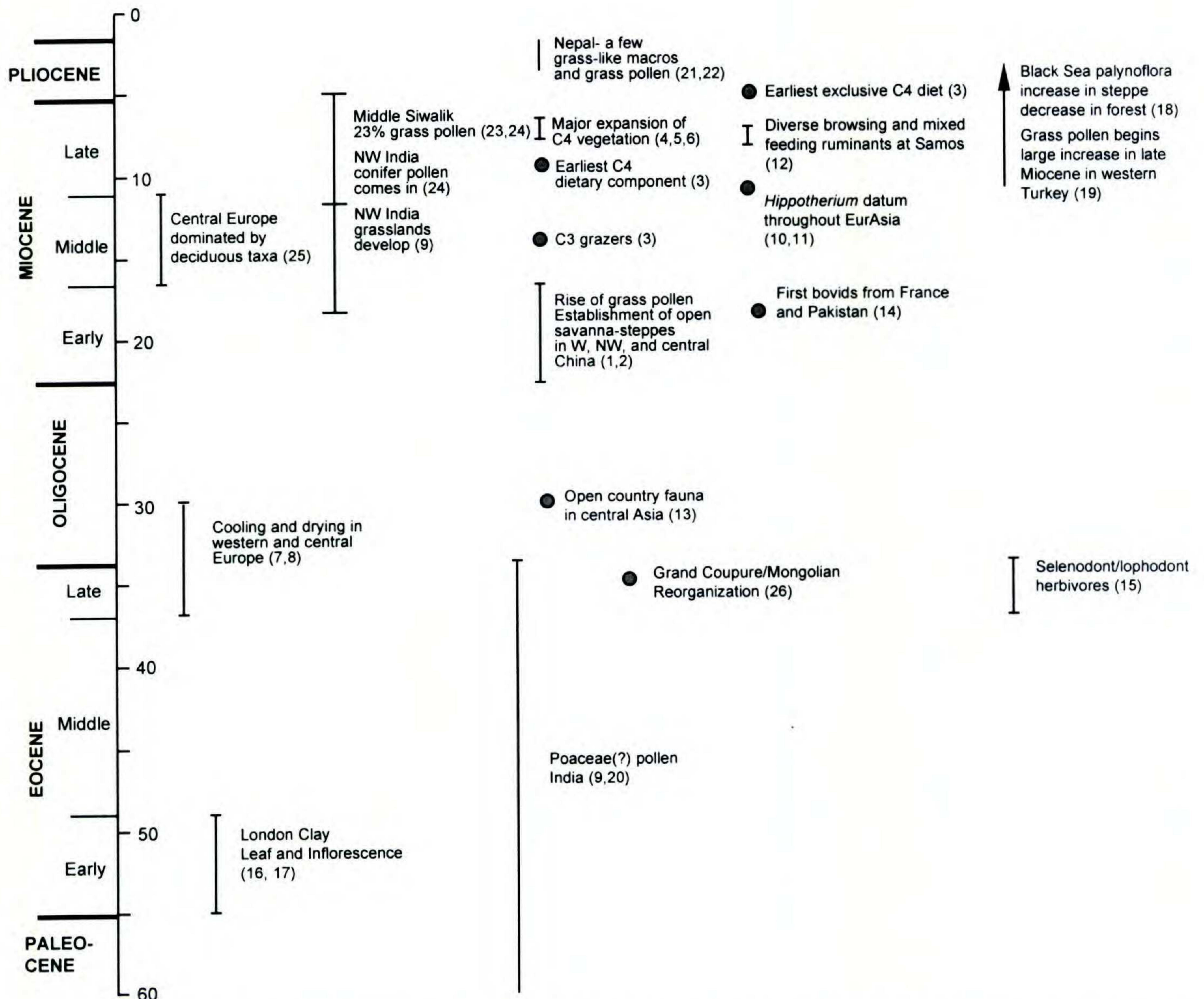


Figure 3. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in Eurasia. Symbols as in Figure 2. Sources: (1) Leopold et al. (1992), (2) Song et al. (1981), (3) Morgan et al. (1994), (4) Quade et al. (1989a), (5) Quade et al. (1995a), (6) France-Lanord & Derry (1994), (7) Collinson (1992), (8) Cavagnetto & Anadon (1996), (9) Mathur (1984), (10) Bernor et al. (1996a), (11) Woodburne (1996), (12) Bernor et al. (1996b), (13) Wang (1997), (14) Solounias et al. (1995a), (15) Jernvall et al. (1996), (16) Chandler (1964), (17) Thomasson (1987), (18) Traverse (1982), (19) Benda (1971), (20) Singh & Sarkar (1990), (21) Prasad & Awasthi (1996), (22) Sarkar (1990), (23) Nandi (1975), (24) Sarkar et al. (1994), (25) Kovar-Eder et al. (1996), (26) Meng & McKenna (1998).

The cooling and drying trend continues into the Neogene. Paleotropical species (e.g., *Tetraclinis salicornoides* Unger, *Daphnogene* sp. Kovar, *Engelhardia orsbergensis* cf. Kovar) are replaced by deciduous, cool-adapted taxa (*Quercus pseudocastanea* Kovar-Eder and ruberoid oaks, *Alnus ducalis* Kovar-Eder, *Acer vindobonensis* Kovar-Eder) from north to south across central, eastern, and southeastern Europe. Thus, there is a time-transgressive and latitudinal trend from evergreen thermophilous taxa in the Paleogene to temperate deciduous forest in the Neogene (Kovar-Eder et al., 1996). Central

Europe was dominated by deciduous taxa by the middle Miocene, while in the southern regions and the western Balkan Peninsula evergreen taxa were abundant until the beginning of the late Miocene (Kovar-Eder et al., 1996; Pantic & Mihajlovic, 1977).

Five middle Miocene pollen samples from lacustrine sediments at Samos Island in the eastern Aegean, dated to 11.2 Ma, are interpreted as representing closed to open woodlands with conifers on nearby uplands (Ioakim & Solounias, 1985). Two samples have 5% and 10% grass pollen, respec-

tively, and the remaining three have none. Ground cover is interpreted to have consisted of a variety of herbaceous plants, including grasses, which were not a significant component of the vegetation.

A continuous core from the Black Sea spanning the last 10 million years provides a large-scale palynological record of vegetation for the more arid interior of eastern Europe, the Ukraine, and north-central Turkey (Traverse, 1982). The late Miocene was dominated by warm-temperate adapted trees such as *Engelhardia* Leschenault ex Blume, *Nyssa*, *Liquidambar* L., oak relatives, and palms (Traverse, 1982). However, a steppe-forest index, consisting of *Artemisia* L. (sage), Chenopodiaceae, and Amaranthaceae pollen, relative to the total pollen flora, indicates the steady spread of steppe beginning 10 Ma and reaching a maximum at the Plio-Pleistocene boundary. Dry, cold climate favors steppe species and grasses, which are inferred to have increased together (Traverse, 1982: 205). A palynological record from western Turkey documents an increase in conifers and herbaceous taxa, including Poaceae, in the late Miocene, with grass becoming very abundant in the middle Pliocene (Benda, 1971).

Asia. The northern and western interior regions of China have grass-dominated, cool, and arid environments today. Paleocene and early Eocene assemblages from north, west, and central China contain significant percentages (as much as 80%) of arid-adapted shrubs, such as *Nitraria* L. and *Ephedra*, sometimes associated with forest taxa, such as *Alnus*, *Betula* L., *Engelhardia*, *Carya*, *Juglans*, and *Liquidambar* (Li et al., 1984; Leopold et al., 1992). Although *Nitraria* and *Ephedra* are abundant, grass pollen in Paleogene samples is rare (Leopold et al., 1992). *Nitraria* remained widespread in the Oligocene, but *Ephedra* retreated to the northwest beginning in the late Eocene (Li et al., 1984). Miocene pollen samples from western and northern China are dominated by herbaceous pollen (as much as 40%) including grass (Leopold et al., 1992) and are interpreted as indicating a broadly open steppe with local forest meadows and pines at higher elevations (Song et al., 1981). Consequently, the Neogene has been classified by Tao (1992) as a "stage of flourishing herbs."

In the Indian subcontinent, Paleocene to Oligocene palynofloral assemblages are reported from northwestern India. Sediments associated with the Paleocene Dras volcanics have a palynoflora interpreted to represent dry, sandy, coastal vegetation based on the occurrence of palms including *Nypa* Steck, together with *Casuarina* L. and *Ephedra*,

with *Carpinus* L., *Corylus* L., and *Carya* derived from uplands (Singh & Sarkar, 1990). Fern spores are also present.

The Subathu Formation of Himachal Pradesh is reported as early to late Eocene by Mathur (1984) and Paleocene-Eocene by Singh and Sarkar (1990). *Graminidites* sp. is reported by Mathur (1984) as rare in the upper Subathu, and Poaceae are reported as present by Singh and Sarkar (1990). The report of Poaceae is probably based on the assumption that *Graminidites* is a grass, although we know of no detailed studies of pollen wall structure and sculpture on these pollen. The vegetation is interpreted as coastal, semi-evergreen, and tropical. Co-occurring taxa include dinoflagellates, palms, *Cycas* L., Betulaceae, Juglandaceae, and the tropical *Anacolosa* (Blume) Blume (Singh & Sarkar, 1990). Samples from the Oligocene Dhamsala Formation are dominated by fern spores with a few angiosperms and no grass pollen reported (Mathur, 1984).

Neogene plant macrofossils and pollen are found in Siwalik and related sediments throughout the foothills of the Himalayas in India and Nepal. Siwalik deposits are the direct result of mountain building associated with the collision of the Indian and Asian plates, and range in age from early Miocene (≈ 22 Ma) to the present (Barry, 1995). The Siwalik sequence of the Potwar Plateau, Pakistan, has precise time control based on the paleomagnetic time scale but contains no paleofloras (Barry, 1995, and references therein). Paleobotanical sites in India are generally designated as lower, middle, or upper Siwalik, and are thus only loosely lithologically correlated to dated sections of the Potwar, or to other vertebrate-bearing sections. The lower Siwaliks of the Potwar Plateau are of early to late Miocene age, ranging from greater than 18 Ma to less than 11 Ma. The superposed middle Siwaliks of the Potwar continue the record into the early Pliocene.

Lower Siwalik wood from the Kalagarh, northeast of Delhi, includes taxa with affinities to Dipterocarpaceae, and the genera *Sterculia* L., *Bursera* Jacq. ex L., *Dialium* L., *Millettia* Wight & Arn., *Diospyros* L., *Artocarpus* J. R. Forst. & G. Forst., and *Ficus* L. (Prasad, 1993). These plants inhabit tropical evergreen or moist deciduous forests today (Prasad, 1993). Lower Siwalik pollen assemblages from northwestern India are dominated by pteridophyte spores and angiosperm pollen, including palm, rare gymnosperms, and approximately 8% *Monoporites* sp. (Banerjee, 1968; Nandi, 1975).

Middle Siwalik pollen assemblages are more species rich than those of lower or upper Siwalik

samples. Most show an increase in gymnosperm pollen (primarily Pinaceae). Macrobotanical sites lack conifers; therefore, conifer pollen is assumed to be allocthonous (e.g., Awasthi, 1982; Prasad & Awasthi, 1996), from upper elevations associated with uplift of the Himalaya (Nandi, 1972, 1975; Ghosh, 1977; Sarkar et al., 1994). Both pollen and macrofossil assemblages indicate increasing seasonality, or decreasing moisture, or both, toward the end of the lower Siwaliks and through the middle Siwaliks, particularly in the northwestern part of the subcontinent (Prakash, 1973). Grass pollen increases to 23% in middle to upper Siwalik sediments (Nandi, 1975; Sarkar et al., 1994). Mathur (1984) interpreted the increase in grass pollen as indicative of established savanna vegetation by the late Miocene (upper part of the middle Siwaliks).

Paleobotanical studies of the Surai Khola Siwaliks, Nepal, are of particular interest because there is a stable carbon isotope record from the same formation (see following isotope section). Plant macrofossils comprise 53 species among 15 families with affinities to extant evergreen and moist deciduous taxa. The proportion of dry deciduous taxa increases toward the top of the middle Siwalik section (Awasthi & Prasad, 1990; Sakar, 1990; Prasad & Awasthi, 1996). Upper Siwalik sediments from Surai Khola are poorly fossiliferous and preserve a few graminoid specimens (Prasad & Awasthi, 1996). Pollen assemblages from the upper Siwalik portion of the sequence include Pinaceae and other wind-pollinated groups, and more than 30% Poaceae in the uppermost sample (*Monoporopollenites kasauliensis*, Singh & Sarkar referred to as "grass pollen," Sarkar, 1990: 322; Prasad & Awasthi, 1996).

PALEOFAUNA

Europe. The European record is, in some ways, similar to that of North America because of direct dispersals via the northern Atlantic region in the early Tertiary and because of dispersals from Asia to Europe and North America throughout the Tertiary (Schmidt-Kittler, 1987; Lindsay et al., 1989; Bernor et al., 1996a). Nevertheless, despite similarities due to episodic faunal exchanges, the records are distinct. The greatest faunal similarity is shown at ≈ 56 Ma (early Eocene; Wasatchian of North America and Sparnacian of Europe), during which time there is no evidence of extensive grass-dominated ecosystems in Europe.

Of major significance in the European faunal record is the Grande Coupure (≈ 34 Ma, early Oligocene), during which the European biota under-

went major reorganization, presumably associated with global cooling. An older vertebrate fauna characteristic of forested environments changed to a younger fauna characteristic of more open, but still relatively closed and wooded, country. Asia was probably a major source for new immigrants in Europe after the Grand Coupure, following removal of the Turgai Straits as a biogeographic barrier.

Detailed data on the chronology and distribution of mammals demonstrate a high degree of regionalism between western Europe, eastern Europe, and southwestern Asia (Bernor et al., 1996a; van Dam, 1997). Fortelius et al. (1996a, b) provided detailed comparisons from about 17 Ma onward between the west (including localities in Portugal, Spain, France, Italy, Germany, Switzerland, Austria, Poland, Czech Republic, and Slovakia) and the east (including localities in Hungary, Slovenia, Serbia, Bosnia, Macedonia, Albania, Greece, Bulgaria, Romania, Moldova, Ukraine, Georgia, Turkey, Iran, Afghanistan, and Kazakhstan). Because such large geographic areas vary locally, the aggregate faunal blocks represent the sum of sampled environments. Nevertheless, there are clearly differences between the two faunal blocks that broadly reflect ecology including the dominant vegetation. Taxon-independent ecomorphological faunal analyses indicate diversity and body size trends from initially closed and forested landscapes toward assemblages characteristic of progressively more open and seasonal environments (Bernor et al., 1996b; Fortelius et al., 1996a, b). Species richness begins to increase in the eastern region at about 10.5 Ma, while it decreases in the west. By the Messinian crisis (approximately 7 Ma and younger), diversity in the eastern region had fallen. For most time intervals from 9.5 Ma onward, the distinctions intensify between the regions with the eastern block fauna reflecting more open conditions than those in the west. This pattern suggests diachronous opening of the landscape, earlier in the east, with central Europe remaining relatively closed (Bernor et al., 1996b; Fortelius et al., 1996a, b).

During the early Miocene (Orleanian, approximately 17 Ma), *Anchitherium* von Meyer (a browsing horse), two genera of proboscideans, and five browsing ruminant artiodactyls are present in Europe. The earliest records of bovids are species of *Eotragus* Pilgrim from Artenay, France, and the Kamliyal Formation, Pakistan, the latter occurrence of similar age to Artenay and dated by magnetic polarity stratigraphy at 18.3 Ma (Solounias et al., 1995a). The genus has a broad distribution throughout Eurasia, Africa, and the Middle East, its youngest record being approximately 14 Ma,

possibly younger. Solounias and Moelleken (1992) examined microwear in *E. sansaniensis* (Lartét) from Sansan, France (15 Ma, Steininger et al., 1996). Microwear on the teeth indicates that this species was a browser. The fauna of Sansan is diverse, including tragulids, suids, cervids, and glirids, among other taxa, suggesting a forest environment. In general, the European faunas of this age indicate a dry subtropical to deciduous forest in the east, with a more closed habitat in the west (Bernor et al., 1996b; Fortelius et al., 1996a, b).

The first appearance of hipparionine horses has traditionally been interpreted as heralding the spread of grasslands across the Old World. In addition, as an abundant and readily identifiable taxon, hipparionine horses hold a fundamental position in Eurasian Neogene mammalian chronology, its first appearance being recognized as the *Hippotherium* Kaup Datum (fide Woodburne, 1996; Woodburne et al., 1996; = *Hipparion* Datum of other authors). Recent studies suggest an origin of *Hippotherium* close to North American *Cormohipparion occidentale* with subsequent dispersal and radiation across Eurasia between about 10.9 and 10.7 Ma (Bernor et al., 1996c; Kappelman et al., 1996; Pilbeam et al., 1996; Woodburne et al., 1996; Sen, 1997). However, the dispersal of hipparionine horses across the Old World may be more complicated than simply the spread of grass-dominated ecosystems as originally interpreted.

Microwear analysis of teeth (Hayek et al., 1992) indicates that North American *Cormohipparion* obtained a significant portion of the diet by grazing. Of the Old World species examined by Hayek et al. (1992), some species were grazers while others appear to have had mixed diets. In hipparionines, reduction of facial fossae (pits on the sides of the muzzle in front of the eyes) is associated with grazing, and retention or elaboration of the facial fossae is associated with those species that appear to be mixed-feeders or to utilize browse. Well-developed facial fossae are retained in early Eurasian *Hippotherium* (Bernor et al., 1996c). Based on the morphology of the limbs, the oldest European hipparionine species were forest dwellers, but later species were adapted for drier and more open country (Eisenmann, 1995). Thus, it appears that the dispersal of hipparionines from North America through Eurasia was associated with factors other than, or possibly in addition to, the spread of grass-dominated ecosystems across the Old World.

The Turolian faunas from the Greek island of Samos, and from Pikermi, near Athens (about 8.3 to 7 Ma; Bernor et al., 1996d), are particularly interesting because they present a diverse fauna that

has historically been interpreted as representing open grassland and savanna, because isotopic studies have been conducted on samples from there (see below; Quade et al., 1994), and because the morphology and tooth wear of several ungulates in the fauna have been analyzed to infer dietary habits. The ruminant fauna consists of approximately 30 species, interpreted to be predominately browsers and mixed-feeders based on the structure of the masticatory apparatus (Solounias & Dawson-Saunders, 1988). More specifically, masseteric morphology of bovids, including two species of *Tragoportax* Pilgrim, two species of *Pachytragus* Schlosser, and one species of *Gazella* de Blainville, indicates mixed-feeding or browsing; however, microwear analysis on the teeth indicates that *Tragoportax* and *Pachytragus laticeps* Andree grazed or at least took grass in the diet seasonally (Solounias & Hayek, 1993; Solounias et al., 1995b). Moreover, premaxillary shape and microwear on the low-crowned teeth of the giraffid *Samotherium boissieri* Forsyth-Major indicates grazing or possibly mixed-feeding (Solounias et al., 1988; Solounias & Moelleken, 1993a, b). In addition, of six species of hipparionine horses for which diet was interpreted from tooth wear (Hayek et al., 1992), three were inferred to be grazers and three mixed-feeders. The mixed-feeders have facial characteristics that may indicate the presence of a proboscis used in gathering browse.

Although the traditional interpretation of the environment of Samos and Pikermi is open grassland, the fauna clearly utilized both browse and grass, and the fauna as a whole does not reflect a pure grassland. Solounias et al. (1995b) suggested that the environment was one of forest and bush country, perhaps analogous to that of the Khana National Park, India, or the Tana River, Kenya (Schaller, 1967; Andrews et al., 1975).

Asia. The trend toward increasing seasonality and open country probably began earlier in China and Mongolia than in the eastern portion of Europe and southwestern Asia. Meng and McKenna (1998) documented an abrupt reorganization from perisodactyl-dominated Eocene faunas to rodent/lagomorph-dominated faunas of the Oligocene, a change they named the Mongolian Remodeling and correlated with the European Grande Coupure (\approx 34 Ma). The cause of the Mongolian Remodeling was suggested to be global cooling, resulting in open environments. The ctenodactylid *Tataromys plicidens* Matthew & Granger from Mongolia, northern China, and Kazakhstan, and other rodents, support an open environment, but not necessarily grass-dominated, in central Asia at 30 Ma (late ear-

ly Oligocene; Wang, 1997). The fauna of the beginning of the Miocene is little different from that of the late Oligocene, although rhinoceroses and other browsing ungulates diversify in the Miocene. Qiu (1989) and Qiu and Qiu (1995) recorded Neogene changes in the Chinese mammal fauna, including the appearance of proboscideans and the browsing horse *Anchitherium* at about 19 Ma (Woodburne & Swisher, 1995), and hipparionines at around 10.8 Ma. Regional variation is indicated especially in the distribution of rodents and primates (Jacobs et al., 1985; Qiu & Qiu, 1995), reflecting a suite of habitats from more forested in the southeast to more open in the interior.

Indo-Pakistan has a complicated geologic and paleogeographic history of northward drift and incorporation into the Asian landmass during the early Tertiary. The Eocene fauna of Indo-Pakistan has some Holarctic elements but includes cetaceans and primitive proboscideans and is deficient in carnivores (Gingerich et al., 1997). The Neogene fauna of Pakistan is representative of a southern Asian zoogeographic province that extended eastward to Thailand (Ducrocq et al., 1994), at least during its middle Miocene portion, changing through time by the dispersal of taxa into the region from Africa and Eurasia and by evolutionary changes occurring within the region. The early Miocene is best represented by the Dera Bugti fauna and characterized by large anthracotheres, deinotheres and gomphotheres proboscideans, and baluchimyine rodents (Raza & Meyer, 1984; Raza et al., 1984; Flynn et al., 1986; Friedman et al., 1992; Downing et al., 1993; Flynn & Cheema, 1994). By 18 Ma, significant microfaunal turnover had occurred (Jacobs et al., 1981; Flynn et al., 1997).

The record from 18.3 Ma through the remainder of the Miocene and into the Pliocene and Pleistocene is preserved in rocks of the Siwalik Group. The Siwalik fauna comprises 13 orders of mammals, although most species are rodents, ruminants, or perissodactyls. The great strength of the Siwalik record is its chronological control, made possible through magnetic polarity stratigraphy, allowing patterns of faunal change to be discerned in detail (Barry et al., 1982, 1985, 1990, 1991, 1995; Flynn & Jacobs, 1982; Jacobs et al., 1989, 1990; Barry & Flynn, 1989; Flynn et al., 1990; Flynn et al., 1995a; Jacobs & Downs, 1994; most recently reviewed by Barry, 1995). With few exceptions (e.g., Flynn et al., 1991; Flynn et al., 1995b; Sotnikova et al., 1997), other Asian faunas lack such precise age control.

Siwalik rodents and artiodactyls increase in diversity between about 15 and 13 Ma, after which

time their diversity decreased. Bovids increase relative to tragulids. By 12.7 Ma, large hominoids appear. Hipparionine horses first occur at 10.7 Ma (Pilbeam et al., 1996), consistent with the first appearances of hipparionines elsewhere in the Old World.

Murine rodents, as represented by *Progonomys* Schaub, occur at about the same time or slightly later than hipparionines in most of Eurasia, but in the Siwaliks *Progonomys* occurs earlier (12.3 Ma). This is an interesting pattern implying that murines evolved in southern Asia. They are now major components of the African savanna fauna, reflecting an endemic radiation, but the initial dispersal of the group from southern Asia may have occurred simultaneously with the dispersal of hipparionines.

In the Siwaliks, murines became numerically abundant but not taxonomically diverse at any given stratigraphic horizon. As a group, striking size increase is apparent by 9.0 to 8.5 Ma and continues less dramatically until at least 8 Ma. Burrowing rhizomyids occur in the Siwalik section prior to 9 Ma, a gerbil (*Abudhabia* de Bruijn & Whybrow also known from the Arabian Peninsula, Flynn & Jacobs, in press) appears briefly at 8.7 Ma, and porcupines (*Hystrix* L.) and rabbits are recorded about 7 Ma. Among rodents, the late Miocene is clearly eventful. Burrowing in rhizomyids and the occurrence of a gerbil and a porcupine are consistent with more open habitat. Four lineages of hypsodont artiodactyls occur from the late Miocene. Faunal change also affects pigs, hippopotamuses, and giraffes in this time interval (Barry, 1995). Hominoids are not recorded in Pakistan after about 8.0 Ma (timescale of Cande & Kent, 1995), and the Siwalik fauna of that age resembles more closely those from northern and western Eurasia (Jacobs et al., 1985; see Qiu, 1989; Qiu & Qiu, 1995).

STABLE ISOTOPES

Analyses of fossil herbivore enamel and paleosol carbonates from middle Miocene to Pliocene sites in the eastern Mediterranean (Quade et al., 1994, 1995b), including Samos and Pikermi (see discussion above), indicate that the vegetation has been dominated consistently by C₃ plants with no evidence of significant C₄ vegetation. Data from Spain and France, as well as North Africa (Cerling et al., 1997b), also indicate that C₄ plants have not been a significant component of the Neogene biomass in western European or Mediterranean biomes.

The spread of C₄ vegetation in Asia appears to have occurred in the late Miocene. This shift was first documented by analyses of paleosol carbonates

collected from the Siwalik sequence in Pakistan, where Quade et al. (1989a) noted an apparent dramatic ecological shift from C_3 - to C_4 -dominated biomass beginning at 7.4 Ma based on the time scale then in use (now calculated at ≈ 8.1 Ma, J. Barry, pers. comm.). They concluded that earlier C_3 biomass was mainly composed of trees and shrubs, whereas C_4 grasslands dominated the Plio-Pleistocene. Paleosol carbonates were collected primarily from floodplain environments, and Quade and Cerling (1995) noted that woodland habitats were probably present throughout this period marginal to the active floodplains. The isotopic transition reflects the replacement of C_3 vegetation (possibly including C_3 grasses) by C_4 grasses. Preliminary analyses of fossil herbivore enamel from the Siwaliks (Quade et al., 1992) indicate C_3 diet at 7.5 Ma and C_4 diet at 3.5 Ma for those taxa surveyed, although data are lacking for the intervening time period. They inferred that, in general, most herbivores examined prior to the isotopic shift were browsers and that the shift reflects displacement of tree and shrub communities on the floodplains of major rivers by nearly continuous C_4 grassland. Isotopic values on tooth enamel younger than 3.5 Ma record only C_4 diet; however, these samples do not include taxa interpreted to have been browsers.

Based on a data set with more complete taxonomic and temporal coverage, Morgan et al. (1994) also recorded the dietary shift from C_3 to C_4 vegetation in fossil herbivores from the Siwaliks, but they concluded that rather than an abrupt transition at 7.4 Ma, the change occurred over a period of 2–3 Ma. In addition, independent evidence for paleodiet based on dental microwear analyses of Siwalik artiodactyl and perissodactyl species, utilized in concert with isotopic data, indicated that C_3 grasses were an integral part of the Siwalik vegetation not only before evidence for C_4 grasses at 9.4 Ma but also subsequent to the transition (Morgan et al., 1994).

Stable carbon isotopic analyses of carbonate in fossil ostrich eggshell from the Siwaliks indicates a dietary shift from C_3 -dominated to mixed C_3/C_4 and pure C_4 diets sometime between 7.5 to 4 Ma (Stern et al., 1994). A scarcity of eggshell data precludes precise conclusions about the timing of this dietary shift. Stern et al. (1994) noted that the dietary shift may have taken place as late as 3.5 Ma and suggested that differences between the timing of mammalian and ratite isotopic shifts may reflect greater dietary discrimination in the mammals.

Isotopic analyses of paleosol carbonates and organic matter from the Siwalik Group in southern Nepal record an ecological change starting ≈ 7.0

Ma (Quade et al., 1995a), 1.1 Ma later than the shift in Pakistan [both dates calibrated to timescale of Cande & Kent, 1995]. This shift is interpreted to mark the displacement of largely C_3 vegetation, probably semideciduous forest, by C_4 grassland in floodplain environments. C_4 biomass prior to the 7.0 Ma transition is interpreted to have been $< 20\%$ of the total. Coincident with this isotopic shift is the decline and final disappearance of leaf fossils and coalified logs from the sequence.

In a more regional examination of this isotopic shift, France-Lanord and Derry (1994) analyzed organic carbon from the Bengal Fan, which also showed a 10‰ increase in $\delta^{13}C$ beginning approximately 7 Ma. This isotopic change indicates that the expansion of C_4 habitats documented in the Siwaliks was widespread over the Himalayan foreland. The relationship between the $\delta^{13}C$ and sediments in the Bengal fan suggest that C_3 plants remained abundant in the Himalayan hinterland throughout the late Miocene and Plio-Pleistocene.

SOUTH AMERICA

SUMMARY

South America spans from about 55°S to 12°N latitude, with great topographic variation, and supports grass-dominated ecosystems over large areas (Fig. 1). Tropical and subtropical savanna, the llanos, is found associated with the alluvial plains of the Orinoco River system and the Guyana region between the Orinoco and the Amazon (Coupland, 1992c). A portion of the tablelands of Brazil, referred to as the campos cerrados, consists of open grassy savanna (campos limpos). A narrow belt of tropical to subtropical grassland occurs at middle elevations along the eastern side of the Andes from Venezuela to northwest Argentina. The largest extent of temperate grassland in South America exists in the Rio de la Plata region of central eastern Argentina (the pampas), Uruguay, and southern Brazil (the campos; Soriano et al., 1992). To the west of this region is woodland to wooded savanna, the chaco of Argentina and Paraguay (Soriano et al., 1992). In the area where Brazil, Bolivia, and Paraguay meet, there is an intermingling of the northernmost extent of chaco woodlands with a southern extension of subtropical savanna (Sarmiento, 1983). High-elevation Andean grasslands of Venezuela and Colombia are referred to as paramo. Argentina and Peru have the intermontane altiplano.

Pollen assemblages from northern South America document *Monoporites annulatus* from the early and late Paleocene (Muller et al., 1987; Rull, 1997; Fig. 4). A pantropical biostratigraphic zone, the *Mono-*

South America

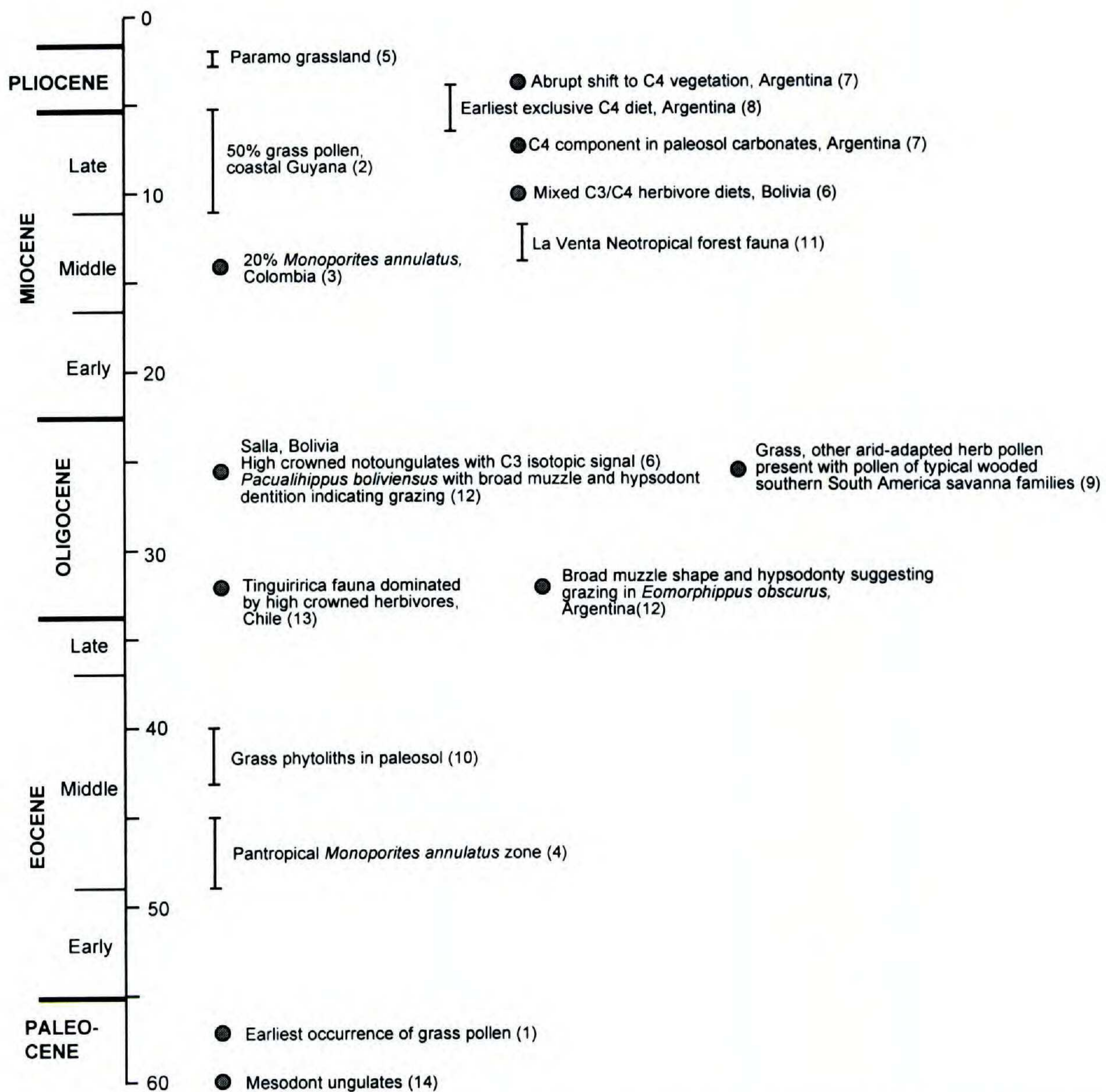


Figure 4. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in South America. Symbols as in Figure 2. Sources: (1) Muller et al. (1987), (2) Van der Hammen & Wymstra (1964), (3) Hoorn (1993), (4) Germeraad et al. (1968), (5) Wijninga (1996), (6) MacFadden et al. (1994), (7) Latorre et al. (1997), (8) MacFadden et al. (1996), (9) Romero (1993), (10) Andreis (1972), (11) Kay et al. (1997a), (12) Shockey (1997), (13) Wyss et al. (1993), (14) Pascual & Ortiz Jaureguizar (1990).

porites annulatus Zone, of late early Eocene (49–45 Ma), recognized by the consistent presence of grass pollen, is widespread in northern South America and western Africa (Germeraad et al., 1968). Several taxa found today in the chacoan wooded savanna, including Poaceae, occur in Oligocene pollen assemblages (Romero, 1993). By the early Miocene, local grass-dominated areas are documented for coastal Guyana (Van der Hammen & Wymstra, 1964; Van der Hammen, 1983), but lowland forest is present in Colombia (Hoorn, 1993; Wijninga, 1996). By the middle Miocene, coastal

savannas are documented in Colombia (Hoorn, 1993). High-elevation paramo grassland is present by the late Pliocene (Wijninga, 1996).

Endemic ungulates (notoungulates) first begin exhibiting increased crown height in the late Paleocene (Pascual & Ortiz Jaureguizar, 1990). The oldest fauna characterized by herbivores with high-crowned teeth is at least 31.5 Ma, and a similar-aged notoungulate has a muzzle shape indicative of grazing (Shockey, 1997). The locality of Salla (27 Ma) contains two notoungulates adapted for grazing based on muzzle shape and hypsodonty. Enamel

samples of high-crowned notoungulates from the Salla section exhibit isotopic signatures consistent with a C₃ diet. The morphology of notoungulates and the known presence of grass in South America both earlier and later than Salla suggest that C₃ grasses may have been a major component in some South American late Oligocene ecosystems.

Evidence for C₄ grasses as a dietary component is first apparent in the enamel of 10 Ma herbivores from Bolivia, which yield isotopic values consistent with mixed C₃/C₄ diets (MacFadden et al., 1994). Exclusively C₄ grass diets are first recorded in the enamel of notoungulates from localities in Argentina (5.5 Ma ± 1 Ma). Paleosol carbonates from Argentina indicate a significant C₄ component in local biomes at 7.3 Ma (LaTorre et al., 1997). The C₄ component increases gradually until 3.7 Ma when there is an abrupt shift to environments comprised of approximately 70% C₄ biomass. There is no unequivocal evidence for C₄ grass-dominated ecosystems earlier in South America than North America. Overall, the vertebrate and isotope data suggest that the initial spread of grass-dominated ecosystems and the coevolution of grazing herbivores involved C₃ grasses as was the case in North America.

PALEOBOTANY

Grass pollen is documented in northern South America during the early and late Paleocene (middle Thanetian, ≈ 57 Ma; Muller et al., 1987; Rull, 1997), although Paleocene records from Argentina lack grass pollen or macrofossils (Menendez, 1971; Archangelsky, 1976). Argentine Paleocene to Eocene palynofloras represent tropical to subtropical forested environments (Menendez, 1971). At the base of the middle Eocene (≈ 48 Ma), Germeraad et al. (1968) defined a palynofloral zone for northern South America (and Africa) marked by the first regular occurrence of *Monoporites annulatus*. This coincides with grass leaf cells preserved in middle Eocene paleosols from the Musters Formation, Argentina (44°S), and interpreted along with pedological features to indicate an environment similar to modern pampas (Andreis, 1972). In addition, the Eocene to Oligocene Sarmiento Formation (≈ 45°S) contains loess units thought to have been formed on an extensive plain (Spalletti & Mazzoni, 1979). Romero (1993) reported the Oligocene occurrence of pollen of Poaceae and arid-adapted herbs (Chenopodiaceae), shrubs (Ephedraceae), and families characteristic of the chacoan woodlands today, suggesting the origin of South American wooded savanna communities at that time. Unfortunately, the

amount of grass cover is not discernible from any of these studies.

Pollen assemblages from the southern tip of Chile (≈ 50°S), estimated to be Eocene to early middle Oligocene in age, are dominated by *Nothofagus* Blume species associated with gymnosperms and ferns (Fasola, 1969). Menendez (1971) noted a northward retreat of tropical floristic elements from Argentina and concomitant expansion of cool-temperate taxa in the late Eocene and early Oligocene. He suggested that significant aridification of the Patagonian region of Argentina did not take place until the late Miocene or early Pliocene as a result of Andean uplift, which would have cut off the source of moist Pacific air masses (Menendez, 1971).

Coastal pollen cores from Guyana document palynological zonation for much of the Tertiary with hiatuses during parts of the Oligocene, Miocene, and Pliocene (Van der Hammen & Wymstra, 1964). *Monoporites annulatus* occurs infrequently in samples from the Oligocene through the Pliocene, and rarely exceeds 10%. However, two samples from the early Miocene section of the Shelter Belt core obtain abundances of more than 10% grass pollen; one contains about 43% grass pollen (Van der Hammen & Wymstra, 1964). Van der Hammen (1983) interpreted these records to indicate savanna similar to that of today in northern South America by the Miocene.

Pollen records from the Colombian Andes of northern South America document substantial uplift of the mountains between the middle Miocene and late Pliocene (Hoorn, 1993; Hoorn et al., 1995; Hoogheemstra et al., 1994; Wijninga, 1996). Early and middle Miocene records from this area contain lowland forest assemblages. However, a noticeable increase from < 10% to 20% in grass pollen occurs in the early middle Miocene (Hoorn, 1993). This is interpreted as representing open grassy areas on alluvial plains (Hoorn et al., 1995). Wijninga (1996) documented the development of high-elevation paramo grassland in the high plain of Bogotá, Colombia, by the latest Pliocene. Palynological records from Central America represent lowland forest on isolated islands until at least the middle Pliocene (Graham, 1987, 1990a, b; see Burnham & Graham, 1999, this issue).

PALEOFAUNA

South America has a reasonably good vertebrate fossil record throughout the Tertiary (Scott, 1913; Webb, 1978; Simpson, 1980; Janis, 1993), with many localities located in what are now grass-dominated ecosystems surrounding the Amazon Basin.

However, fossil localities reflect latitudinal and orographic effects, just as the modern biota does.

The earliest record of hypsodonty among mammals, not just within South America, but globally, is found in Late Cretaceous and early Tertiary sudamericid gondwanatheres. This group has been considered related to multituberculates. Gondwanatheres are known from South America, Madagascar, and India, probably reflecting Late Cretaceous continental connections through Australia and Antarctica (Woodburne & Case, 1996; Krause et al., 1997). Other diverse multituberculates, all herbivores, have a geographically broad distribution in the Northern Hemisphere throughout the Cretaceous and early Tertiary, but no others, except gondwanatheres (if they are in fact multituberculates), developed high-crowned teeth, so far as is currently known. Hypsodonty, in the case of gondwanatheres, may indicate abrasive diet as in many other mammals with high-crowned teeth, but in any case, these small mammals first occur prior to the earliest fossil record of grasses.

The Tertiary record of mammals in South America is characterized by a number of endemic, increasingly high-crowned notoungulates and other taxa at least from the late Paleocene (Webb, 1978; and references therein; Cifelli, 1985; Pascual & Ortiz Jaureguizar, 1990). Pascual and Ortiz Jaureguizar (1990) reviewed faunal change as related to climate based on a multivariate analysis of South American land-mammal ages (SALMA), and using cheek tooth characters, particularly of ungulates, to indicate dietary preferences. Notoungulates with teeth becoming hypsodont first appear in the Paleocene (Riochican, approximately 60 Ma). High-crowned *Sudamerica* Scillato-Yané & Pascual, a gondwanathere, is also recorded in the Riochican.

From the Paleocene through most of the Tertiary the percentage of ungulates with higher-crowned teeth increased. The latest Eocene-early Oligocene Tinguiririca fauna of Chile (at least 31.5 Ma, possibly extending to 37 Ma; Flynn & Swisher, 1995) is dominated by high-crowned herbivores (Wyss et al., 1993). Shockey (1997) reported that the notoungulate *Eomorhippus obscurus* Ameghino from the Cañadón Blanco locality, Argentina, which he considers roughly the same age as the Tinguiririca fauna, has hypsodont teeth and a broad muzzle characteristic of grazers.

By 27 Ma (Deseadan, late Oligocene; Kay et al., 1997; MacFadden et al., 1985; Naeser et al., 1987), *Pascualhippus boliviensis* Shockey, another notoungulate with hypsodont teeth and a broad muzzle characteristic of grazers, was present at Salla, Bolivia (Shockey, 1997). The environment of Salla has

been interpreted as being semiarid because of the large percentage of species with high-crowned teeth. The Salla primate *Branisella* Hoffstetter has features similar to ground-dwelling monkeys. The oldest known argyrolagid (*Proargyrolagus boliviensis* Wolff) is from Salla (Sánchez-Villagra & Kay, 1997). It is similar to elephant shrews, but has higher-crowned teeth, suggesting that it included seeds or other plant material gathered on the ground in its diet. The nasal region of *Proargyrolagus* is similar to that seen in desert heteromyid rodents.

The diverse Miocene fauna from La Venta, Colombia (13.5–11.8 Ma; Madden et al., 1997), is reviewed in Kay et al. (1997a). The site is located in what was at the time a Miocene peninsula in the equatorial tropics. Kay and Madden (1997) summarized the evidence for a forest environment, including the presence of a fish that exploits periodically flooded forest, forest reptiles and birds, diverse arboreal marsupials, sloths with climbing adaptations, mostly low-crowned ungulates, forest-dwelling bats, and arboreal monkeys. Five genera of primates are known from the Monkey Unit at La Venta, the number of sympatric genera today characteristic of neotropical forest receiving 1500–2000 mm annual rainfall (Kay et al., 1997b; Fleagle et al., 1997). Of the approximately 80 species of mammals recorded, only one has been suggested to be a grazer, and that is the large and rather aberrant toxodontid notoungulate *Pericotoxodon platignathus* Madden (Madden, 1997).

Ecological variation across the continent is indicated because ungulates at higher latitudes are in general more hypsodont than those at lower latitudes. Taken as a whole, middle to late Miocene diversity declined in most of South America, although hypsodont mammals seem to prevail. Caviomorph rodents, which are the only rodents occurring in South America until the Pliocene (3.5 Ma; Jacobs & Lindsay, 1984; Baskin, 1986), have fundamentally lophodont and relatively high-crowned teeth, even among the early members of the group. Their first occurrence is in the Tinguiririca fauna. During the Miocene their diversity increased, reaching a maximum in the late Miocene. The general trend in rodents was toward increased height of tooth crown and increased body size, some reaching exceptionally large size, and filling grazing niches (Simpson, 1980; Vucetich, 1984, 1986; Cifelli, 1985). After about 3 Ma, grazing horses and proboscideans entered South America via the Panamanian land bridge.

The early and widespread development of hypsodonty in South American ungulates (compared to

North American ungulates) as a response to a diet of grass has long been debated (Patterson & Pascual, 1972; Simpson, 1980; Stebbins, 1981). The mammalian fossil record is consistent with the presence of a significant grass component throughout most of the Tertiary in South America. Grass sufficient to support true grazers was present in the west-central portion of the continent, and by extension, at higher latitudes, by 27 Ma. By 31.5 Ma (minimum estimate), the Tinguiririca fauna may represent woodland or savanna grasslands as suggested by Flynn and Swisher (1995; see also Wyss et al., 1993).

STABLE ISOTOPES

Isotopic evidence for the spread of C_4 biomes in South America suggests a more complex transition to C_4 vegetation than seen in North America. Analyses of the enamel of high- and low-crowned endemic notoungulates and pyrotheres (another endemic ungulate group), as well as immigrant taxa, from Oligocene to Pleistocene fossil localities in Bolivia indicate mixed C_3/C_4 diets by about 10 Ma (MacFadden et al., 1994). Exclusively C_4 diets are not documented until the Pleistocene. Estimated paleoelevations for the middle to late Miocene Bolivian sites are 1800 m or less. MacFadden et al. (1994) concluded that if C_4 grasses were widespread they would be detected isotopically. The high-crowned dentition of notoungulates from the site of Salla (27 Ma) are interpreted as grazing adaptations (see discussion of *Pascualhippus boliviensis* above), suggesting that the C_3 dietary signal reflects the presence of C_3 grasses.

Paleosol carbonate and fossil enamel from sediments exposed in northwest Argentina indicate that although C_4 grasses were present as a dietary component by 7.6 Ma, C_4 -dominated habitats were not apparent in the local landscape until about 3.7 Ma (Latorre et al., 1997). Paleosol carbonates show a gradual increase in the C_4 component starting 7.3 Ma with a sharp increase in C_4 biomass at about 3.7 Ma, interpreted as indicating 70% C_4 cover.

Carbon isotopic analyses of 65 fossil mammal tooth specimens from a number of low- to middle-elevation sites in Argentina ranging from late Oligocene to late Pleistocene also provide evidence for a late Miocene carbon shift (MacFadden et al., 1996). Their data show that herbivore enamel samples older than the Huayquerian SALMA (9–6.5 Ma) exhibit exclusively C_3 dietary signatures. During the Huayquerian, more positive $\delta^{13}C$ values of mammalian enamel indicate mixed C_3/C_4 in addition to pure C_3 diets. Exclusively C_4 diets are first

apparent in herbivores of Montehermosan age (6.5 to 3.9 Ma). Preliminary analyses of the $\delta^{13}C$ composition of high-crowned mammals younger than 8 Ma collected from lowland sites spanning about 15° of latitude in Argentina and Bolivia indicate an isotopic gradient proportional to latitude. Paleoenvironmental reconstructions range from open C_4 grasslands at low-latitude sites (21° to 27°S) to mixed C_4 grassland/ C_3 browse habitats at higher-latitude sites (\approx 35°S).

AFRICA

SUMMARY

The modern savannas and grasslands of Africa are among the best known in the world because of the spectacular mammalian communities associated with them. A large portion of the African continent consists of grass-dominated ecosystems (Fig. 1). Semi-desert grassland occurs to the north and south of the Sahara. In central Africa, grassland savanna to woodland occurs north, south, and east of the equatorial forests. Grass-dominated environments continue into southern Africa and are widespread except in the Namib and Kalahari deserts, the southeastern coastal forest zone, and the unique sclerophyllous shrub communities (fynbos) of the South African Cape (White, 1983). Highveld grassland occurs on the high (1220–2150 m) plateau of the interior of South Africa.

The earliest record of grass in Africa is the occurrence of *Monoporites annulatus* in Paleocene pollen samples from Nigeria (Fig. 5). A core from coastal Cameroon and a Miocene to Pleistocene core from the Niger Delta document forest communities beginning in the Oligocene and expansion of grass-dominated communities beginning in the middle Miocene (Salard-Cheboldaef, 1979, 1981; Morley & Richards, 1993).

The macrofloral record in eastern Africa documents a range of early to late Miocene environments including woodland or wooded savanna and wet and dry forests (Chaney, 1933; Chesters, 1957; Hamilton, 1968; Yemane et al., 1985; Jacobs & Kabuye, 1987; Jacobs & Deino, 1996), consistent with paleosol isotopic signals indicative of mixed C_3/C_4 environments (Kingston et al., 1994). Grass pollen and macrofossils occur at Fort Ternan, Kenya, dated at 13.9 to 14.0 Ma (Shipman et al., 1981), a site with a rich mammalian fauna consistent with a heterogeneous landscape. Abundant grass pollen in East African Pliocene samples indicates the presence of widespread grass-dominated environments by that time (Bonnefille, 1995).

The vertebrate record of the East African early

Africa

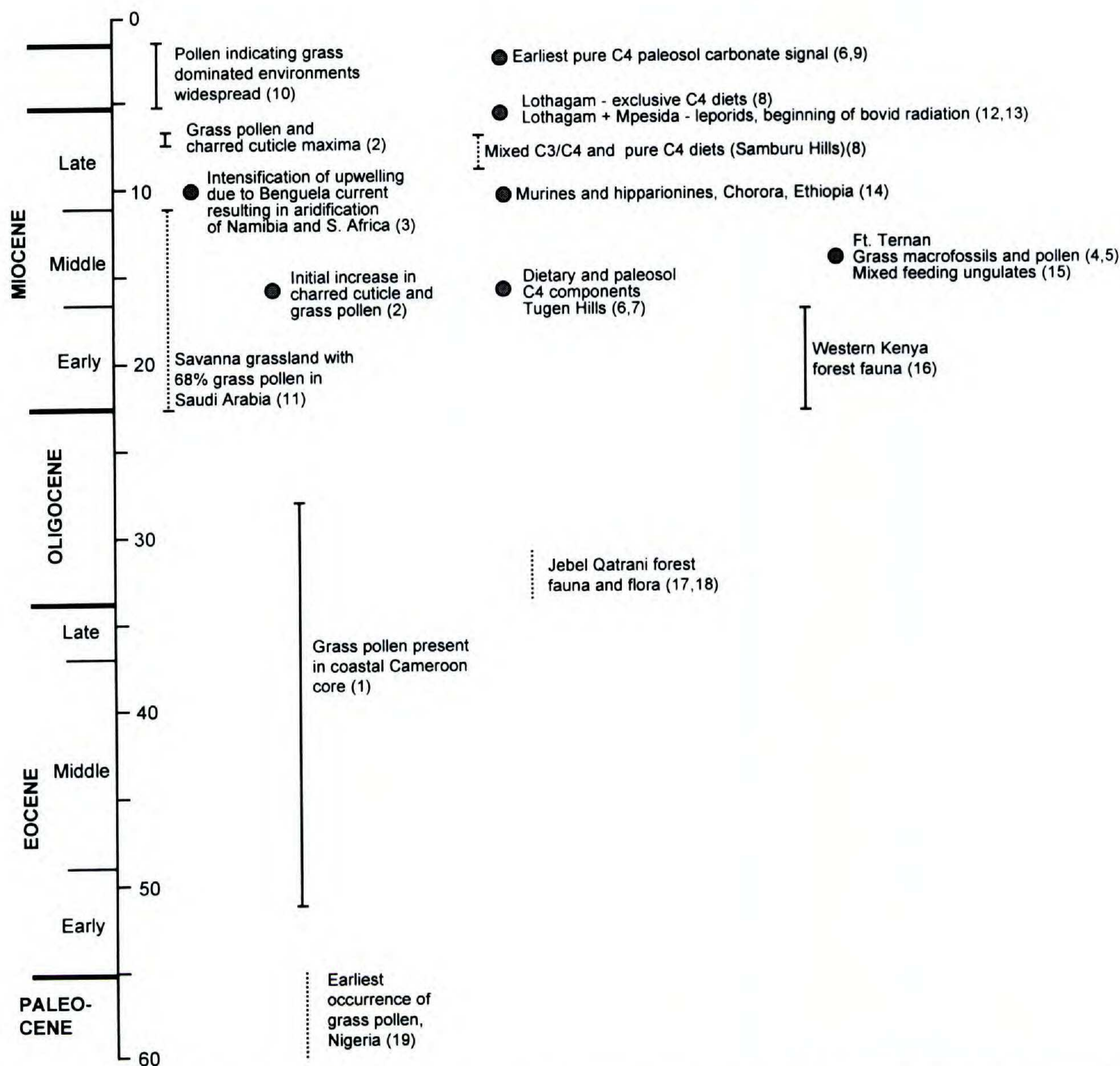


Figure 5. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in Africa. Symbols as in Figure 2. Dashed lines indicate temporal uncertainty for the locality. Sources: (1) Salard-Cheboldaef (1979, 1981), (2) Morley & Richards (1993), (3) Siesser (1978), (4) Dugas & Retallack (1993), (5) Bonnefille (1984), (6) Kingston et al. (1994), (7) Morgan et al. (1994), (8) Leakey et al. (1996), (9) Cerling (1992), (10) Bonnefille (1995), (11) Whybrow & McClure (1981), (12) Leakey et al. (1996), (13) Vrba (1995), (14) Hill et al. (1985), (15) Cerling et al. (1997a), (16) Andrews et al. (1997), (17) Rasmussen et al. (1992), (18) Bown et al. (1982), (19) Adegoke et al (1978).

Miocene indicates a variety of mixed habitats, giving way to more open, but still mixed, environments by at least 15 Ma. A major change in the East African fauna occurs between 8.5 and 6.5 Ma (Hill, 1995; Leakey et al., 1996), including the first introductions of high-crowned rabbits and porcupines, and significant turnover in hippos, giraffes, bovids, rhinos, and elephants. Rodents with high-crowned teeth in Namibia indicate more open conditions in southwestern Africa than in the eastern

portion of the continent during the early part of the Miocene. Regional differentiation is also evident at approximately 5 Ma.

Based on isotopic analyses of fossil herbivore enamel collected from the northern Kenya rift valley, a C₄ dietary component is evident by middle Miocene times (Morgan et al., 1994), but it is not until the late Miocene that there is evidence for significant intake of C₄ biomass. Paleosol data from the Tugen Hills also indicate that C₄ plants com-

prised a minor part of the local ecosystems by middle Miocene times (Kingston et al., 1994). Interestingly, there is no unequivocal paleosol data from East Africa indicating C₄-dominated ecosystems similar to the modern Serengeti grasslands until well into the Pliocene (Cerling, 1992; Kingston et al., 1994).

PALEOBOTANY

Africa has an interesting paleobotanical record derived from macrobotanical remains of leaves, fruits, seeds, and wood that provide a detailed view of local vegetation, marine cores that provide a large-scale view of vegetation change on land from pollen and cuticle transported out to sea, terrestrial pollen assemblages that sample at an intermediate scale between marine cores and macrobotanical sites, and indirect evidence of past vegetation change based on modern plant systematics and biogeography. The marine cores provide data relevant to the origin of grass-dominated ecosystems in equatorial Africa because they are continuous over long time intervals and sample a broad region; macrobotanical and terrestrial pollen sites reflect more local vegetation and are discontinuous through time and space.

Monoporites annulatus pollen is first found in Africa in sediments of the Kerri-Kerri Formation of Nigeria. The taxonomic composition of this assemblage was used to determine that the formation is Paleocene in age (Adegoke et al., 1978).

Pollen contained in core sediments from coastal Cameroon document the presence of *Monoporites annulatus* pollen in early Eocene assemblages described as "... une quantité relativement importante de Monocotyledones (Gramineés et Palmiers) ..." (Salard-Cheboldaeff, 1981: 412; 1979). The same pollen zone is identified in South America. Interestingly, grass pollen drops out of the African core record from the middle Oligocene to the early Miocene, the limit of the core (Salard-Cheboldaeff, 1979). Concurrent with the disappearance of grass pollen is an increase in forest taxa diversity documenting the spread of lowland tropical vegetation in West Africa during the middle Tertiary (Salard-Cheboldaeff, 1981).

A core from the Niger Delta beginning in the early Miocene and continuing to the Holocene documents changes in extent of West African savanna, and by inference, changes in aridity, based on grass pollen and charred grass cuticle assumed to be from a savanna environment (Morley & Richards, 1993). Earliest Miocene sediments in the core contain about 2% grass pollen and no charred cuticle.

The pollen percentage increases to about 10% and charred cuticle to about 2% by 16 Ma. With some variation, these relative percentages remain 15% or less until a hiatus between 11 and 8.5 Ma. After 8.2 Ma both grass pollen and charred cuticle increase substantially. During the late Miocene grass pollen fluctuates between a few percent to just over 50%. There are two late Miocene maxima of charred grass cuticle (25 to 30%) at about 7.5 and 6.8 Ma. Grass pollen decreases markedly at the base of the early Pliocene but increases again around 4.5 Ma. Pleistocene relative percentages of grass pollen are over 40% with maxima approaching 60%. Charred cuticle does not exceed 20%. This record is interpreted as indicating an equable, wet climate during the early Miocene when little or no grass-dominated vegetation would have been present in West Africa. An expansion of grass cover is inferred for the middle Miocene (\approx 16 Ma), but its extent is difficult to determine. The high percentages of grass pollen and charred cuticle during the late Miocene indicate periods of marked aridity with strong seasonality of rainfall. Savanna extended over most of the Niger Delta (Morley & Richards, 1993).

Deep Sea Drilling Program cores 363 and 362 off the coast of Namibia document the development of upwelling associated with the Benguela Current, which today is responsible for dry air masses and Namibia's arid climate (Siesser, 1978). On the basis of diatom productivity and sedimentation rates, cold upwelling was weak and sporadic from the late Oligocene to the middle Miocene, intensifying markedly around 10 Ma. Aridification of the Namib Desert may have begun at this time (Siesser, 1978), a hypothesis consistent with the Namibian vertebrate record.

Plant macrofossils of Oligocene age from the Jebel Qatrani Formation, Fayum Depression, Egypt, have affinities with extant Indomalaysian and African taxa. The assemblage represents a forest on the southern shore of the Tethys (Bown et al., 1982). The flora includes *Cynometra* L., a genus with several extant mangrove species.

Pollen core samples from coastal Saudi Arabia are attributed to the early Miocene Dam or middle Miocene Hofuf formations, which are indistinguishable in the subsurface (Whybrow & McClure, 1981). One of five samples contains primarily terrestrial pollen, including 68% grass and 26% non-forest taxa. The other four samples are dominated by pollen of aquatic vegetation and grasses. Together with fossil root casts identified as from mangrove plants in the Dam Formation, the assemblages are interpreted as representing an inland sa-

vanna grassland and a coastal region with freshwater marshes and mangrove vegetation. The rainfall regime is considered to have been seasonal, perhaps monsoonal (Whybrow & McClure, 1981). More recent examination of the same root casts (Whybrow et al., 1990) has revealed morphology with affinities to the family Fabaceae, which includes plants adapted to a wide variety of environments including coastal settings.

Early Miocene plant macrofossil sites from East Africa preserve both wet and dry forest, and in some cases, woodland assemblages. Leaf and wood floras from the eastern and western Ethiopian Plateau include dry forest taxa having affinities with modern Central and West Africa (Lemoigne et al., 1974; Lemoigne, 1978). Wood from Welkite, Ethiopia, shows semi-diffuse porous wood, crystals in parenchyma cells, and evidence of fire trauma, indicating a seasonally dry environment (Lemoigne, 1978). The Ethiopian sites are not dated radiometrically, but are considered early Miocene based on stratigraphic position and by comparison with other African Tertiary floras.

Flowers, fruit, and leaves from Bukwa, Uganda, underlie a 22 Ma volcanic flow (Walker, 1968, 1969; Brock & Macdonald, 1969). The assemblage has taxa with affinities to extant Ugandan forest trees such as *Bersama abyssinica* Fresen. (Melianthaceae) and *Cola cordifolia* (Cav.) R. Br. (Sterculiaceae, Hamilton, 1968). Another horizon at Bukwa contains an autochthonous leaf bed consisting primarily of grasses not identified below the family level. However, rhizomes identified as *Juncellus laevigatus* (L.) C. B. Clarke demonstrate the presence of an alkaline lake and indicate that the associated grasses are near-shore or aquatic (Hamilton, 1968).

The Bugishu flora of Uganda occurs in association with early Miocene volcanics of Mt. Elgon and contains leaves, fruit, and wood (Chaney, 1933). A total of 12 taxa comprise genera found today in dry forest or woodland. The ecology of modern relatives and the relatively small size of the leaves (when compared to Eocene leaves studied by Chaney) led to the conclusion that the flora represents savanna or savanna woodland with a dry season, although no grass fossils are reported from Bugishu (Chaney, 1933).

A small leaf flora from the Republic of Congo is considered middle Tertiary in age and is dominated by the monotypic palm genus *Sclerosperma* Mann & H. Wendland today found only in swampy areas of Central and West Africa (Lakhanpal, 1966). A wood assemblage from the Republic of Congo, associated with early Miocene mammalian fossils,

contains four Fabaceae and two Meliaceae species (Lakhanpal & Prakash, 1970). Nearest living relatives occur in wet or dry forests. Two of the fossils are related to genera having species that occur in woodlands today.

The largest and most diverse assemblage of plant macrofossils from the early Miocene of equatorial Africa comes from Rusinga and Mfwangano islands, Lake Victoria, Kenya (Chesters, 1957). The age of the localities is 17.8 Ma (Drake et al., 1988). The flora contains several tree taxa found today primarily in wet forests of Central and West Africa. The abundance of lianas (half of the reported species) was taken by Chesters (1957) to indicate gallery forest, although the flora has been reinterpreted as indicating lowland wet forest (Andrews & Van Couvering, 1975).

The middle Miocene paleobotanical record of Kenya is represented by Ft. Ternan in western Kenya, and Kabarsero, in central Kenya. The fauna of Ft. Ternan, dated at 13.9–14.0 Ma (Shipman et al., 1981), has been studied extensively. A pollen assemblage is dominated by grass pollen (54%), with the remainder of the spectrum being aquatic and montane species (Bonnefille, 1984). The pollen of montane species are interpreted to have come from nearby volcanic highlands, while the local vegetation was an open woodland. An autochthonous assemblage of grass blades preserved in volcanoclastic sediment has been interpreted as representing Africa's earliest wooded grassland flora and compared with the modern Serengeti (Retallack et al., 1990; Dugas & Retallack, 1993), which is populated currently by C₄ grass species. Ft. Ternan grass specimens were assigned to five extinct species in three extant genera, two of which are C₄, and one of which is C₃ today (Dugas & Retallack, 1993). Carbon isotope studies of paleosols at Ft. Ternan document a strong C₃ signal, which indicates a minor role at best for C₄ grasses (Cerling et al., 1991, 1997a). This discrepancy between a paleoenvironment consisting of widespread C₄ grasses (as interpreted based on the grass fossils), and the C₃ carbon isotope signal may indicate that the fossil grasses were not C₄ photosynthesizers (but some possessed epidermal morphology similar to living C₄ species), or that C₄ species were uncommon in the plant community and had little or no effect on the isotope signal. Given that the fossil-bearing exposures at Ft. Ternan are limited to < 200–300 m², the aerial extent of this past community is not known; thus, the scale implied by use of the Serengeti as a modern analogue may be inappropriate.

The Tugen Hills, a mountain range within the eastern rift in central Kenya, contains fossiliferous

sediments that range in age from 16 Ma to the present. Fossil plant localities occur at 12.6, about 9.0, and 6.8 Ma. The oldest, Kabarsero, is an autochthonous assemblage of leaves, twigs, and fruit from a moist forest with taxonomic affinities to Central and West Africa (Jacobs & Kabuye, 1987, 1989; Jacobs & Winkler, 1992; Jacobs & Deino, 1996). Waril (\approx 9 Ma) contains a lacustrine assemblage of seasonally dry vegetation similar to that found associated with wooded savanna today; however, no grass fossils are known from this assemblage.

The late Miocene Kapturo site (6.8 Ma) consists of an assemblage of leaves of deciduous woodland or dry forest taxa (Jacobs & Deino, 1996), but no grass has yet been found. An approximately contemporaneous site from about 10 km to the southeast of Kapturo, the Mpesida forest, preserves abundant fossil wood in volcanic matrix. Preliminary identifications indicate affinities with Central and West African forest taxa, some species of which occur in montane settings today.

A sequence of lacustrine pollen samples from the Chilga region of the Ethiopian Plateau overlies a volcanic unit dated at 8 Ma (Yemane et al., 1985). The assemblages contain abundant wet lowland forest taxa with affinities to extant Central and West African flora. Grass pollen grains, present in some of the 46 spectra, occur in low percentages when compared with modern East African savanna soils and never exceed 27%.

Pollen samples from a variety of East African Pliocene localities consistently contain high percentages ($>$ 50%) of grass pollen (Bonnefille, 1995), indicating a background of widespread grass-dominated environments. Changes in the amount and composition of relatively less abundant arboreal pollen indicate variations in the extent of woodland and forest vegetation (Bonnefille, 1995, and references therein).

Biogeographic analyses of extant equatorial African plants and animals document disjunctions between the coastal forests of East Africa and those of Central and West Africa. Because disjunctions occur at more than one taxonomic level in plant families (Faden, 1974), butterflies (Carcasson, 1964), and birds (Moreau, 1966), more than one period of isolation between the forests of East and Central Africa is likely. Faden (1974) postulated that the initial biogeographic isolation of the two regions took place during the middle Miocene when a nearly continuous equatorial forest belt is thought to have been replaced in East Africa by more xeric plant communities such as those found between forest remnants today (see also Carcasson, 1964; Andrews & Van Couvering, 1975; Axelrod & Raven,

1978). However, the variety of environments now known from the Miocene of the rift valley do not support a simple unidirectional breakup of continuous forest in the middle Miocene. Rather, a more heterogeneous landscape is likely throughout the Miocene in both time and space.

Paleogene and early Neogene plant fossils are uncommon in South Africa. Chronological control is especially difficult. Nevertheless, probable early Miocene pollen and macrofossil localities are interpreted as indicating subtropical woodland with swamps for the southwestern Cape, and subhumid subtropical woodland for northwest South Africa (Scott, 1995). Aridification of these regions is associated with the intensification of the Benguela Current in the early late Miocene (Coetzee, 1978; Scott, 1995).

PALEOFAUNA

The Tertiary vertebrate record of Africa (including the Arabian Peninsula) is sporadic and discontinuous (Winkler & Jacobs, 1993). Paleogene localities are concentrated in the far north with only one locality of early Oligocene age found south of the Equator (in Angola, Rasmussen et al., 1992), and its composition is consistent with localities farther to the north. At least 23 mammalian species, including the primate *Altiatlasius* Sigé, Jaeger, Sudre & Vianey-Liaud, are known from the Late Paleocene of the Ouarzazate Basin, Morocco (Sigé et al., 1990; Gheerbrant, 1992, 1994, 1995). The fauna includes endemic taxa but shows affinities with Europe and North America. All of the specimens are small, suggesting to Gheerbrant (1995) that the fauna was hydrologically sorted and biased against large specimens. Marsupials, elephant shrews, primates, and hyracoids, as well as endemic rodents and other taxa occur in Eocene faunas (Rasmussen et al., 1992; Court, 1993a).

The best known and most diverse African Paleogene fauna is that of the Jebel Qatrani Formation of the Fayum Depression, Egypt, constrained by a radiometric age of 31 Ma on an overlying basalt (Fleagle et al., 1986; Bown & Kraus, 1988). The Jebel Qatrani Formation spans the Eocene-Oligocene boundary and produces fossils of both late Eocene and early Oligocene age (Van Couvering & Harris, 1991; Rasmussen et al., 1992). At least 43 mammalian genera are known, including marsupials, pangolins, ptolemaiids, elephant shrews, primates, rodents, carnivorans, hyracoids, anthracotheres, proboscideans, and arsinotheres (Van Couvering & Harris, 1991; for species, see Bown et al., 1982, who listed 70 mammalian species plus

over 20 species of other vertebrates). Within this suite, primates, hyracoids, and rodents are particularly diverse. The environment of the Jebel Qat-rani Formation has been studied from a number of perspectives and appears to represent mangrove swamps near the coast, giving way to forest. This is consistent with the diversity of arboreal primates and other taxa.

The recent analysis of the postcranial skeleton of *Arsinotherium* Beadnell by Court (1993b) is interesting because of the large size and heavy dental wear of this taxon, which was previously interpreted as indicating arid savanna. However, Court (1993b) showed that the hindlimbs and pelvic girdle were weak in comparison to other large terrestrial mammals, that the forelimbs were capable of movement consistent with propelling the body forward in subaqueous locomotion, and that the limbs were graviportal with spreading feet. *Arsinotherium* was not built for prolonged terrestrial locomotion, but rather lived much of its life in water, moving by antebra-chial extension and brachial retraction, its hind legs trailing behind. Its locomotion on land was not ambulant, but a slow rolling progression over soft wet substrates. Furthermore, the dentition may indicate a specialized method of browsing not represented among modern herbivores (Court, 1992; Janis, 1995).

The early Miocene in western Kenya is well known from such sites as Meswa Bridge, Mteitei Valley, Koru, Legetet, Chamtwara, Songhor, Mfwangano, and those on Rusinga Island, ranging in age from ≈ 23 Ma to ≈ 17 Ma. The faunas from these sites are not uniform, but all appear to represent forested environments based on mammalian community structure and indicator species (Andrews & Van Couvering, 1975; Van Couvering & Van Couvering, 1976; Andrews et al., 1979; Evans et al., 1981; Drake et al., 1988; Savage, 1989). The faunas are characterized by the presence of diverse primates, scaly-tailed flying squirrels, and various other rodents, tenrecids (Jacobs et al., 1987), elephant shrews (including the earliest record of the extant genus *Rhynchocyon* Peters (Novacek, 1984), tragulids, and other taxa.

Forest faunas characterize the beginning of the middle Miocene as well, although early middle Miocene faunas are not homogeneous and vary from site to site (Hill et al., 1991; Winkler, 1992). By 14.7 Ma (Feibel & Brown, 1991), the fauna from Maboko, with its relative abundance of the browsing artiodactyl *Climacoceras* MacInnes, reduction in the number of forest species, relatively abundant monkeys, and derived rodents, suggests woodland

(Andrews et al., 1981; Evans et al., 1981; Winkler, 1997, 1998).

The middle Miocene site of Fort Ternan (13.9–14.0 Ma, Shipman et al., 1981) is important because it has a diverse fauna of approximately 48 species, including primates. Its environmental interpretation has become central to the issue of east African forests opening up into grass-dominated ecosystems (see Andrews & Evans, 1979; Evans et al., 1981; Kappelman, 1991; Shipman, 1986). Most recently, tooth microwear in the giraffid *Palaeotragus primaevus* Churcher and the bovids *Kipsigicerus labidotus* Thomas and *Oioceros tanyceras* Gentry from Fort Ternan was examined (Cerling et al., 1997a). *Kipsigicerus labidotus* and *O. tanyceras* are the two most common species in the fauna. Muzzle shape in *Palaeotragus* Gaudry and *Kipsigicerus* Thomas was also evaluated. Results indicate that *Palaeotragus* and *Oioceros* Gaillard were browsers, although *Oioceros* may have had habits similar to that of the common waterbuck, an extant species atypical in being adapted to grazing near waterlogged habitats. *Kipsigicerus* was a mixed-feeder, meaning that it would both browse and graze. Thus, grass may have made up part of the diet in *Oioceros* and *Kipsigicerus* at Fort Ternan (Cerling et al., 1997a), a conclusion consistent with the interpretations of Shipman (1986) and Shipman et al. (1981).

The sequence of middle Miocene localities in the Baringo Basin, Kenya, provides a well-calibrated, if sporadic, record between ≈ 13 Ma and 6 Ma, which documents a number of significant faunal changes. Hipparionine horses first occur in the Baringo sequence at Ngeringerowa (Hill et al., 1985), considered to range in age from 9.5 to 8.5 Ma (Hill, 1995), consistent with the age suggested by Flynn and Sabatier (1984) based on the relationships of rhizomyid rodents. The Ngeringerowa record of hipparionines is younger than the accepted date of 10.5 Ma for the Chorora Formation of Ethiopia, which contains both hipparionines and murine rodents (Jacobs, 1985; Winkler, 1994). In North Africa, the first record of hipparionines and the murine *Progonomys* is at Bou Hanifia, Algeria, which Woodburne et al. (1996) suggested may be as young as 9.5 Ma, although its lower age limit is set by an underlying radiometric date of approximately 12 Ma. The significance of murine rodents is that, from their introduction into Africa in the middle Miocene to the present day, they have generated a current diversity of over 100 species, and they are the most abundant group of rodents inhabiting African grass-dominated ecosystems. Their evolutionary history in Africa is closely tied to the development

of those ecosystems, even to the extent that in the modern Serengeti grasses as food resources are partitioned between ungulates and the African grass rat (*Arvicanthus niloticus* Lesson), a murine (Senzota, 1983). Nevertheless, in the fossil record, the faunas of the Baringo Basin do not indicate the clear and consistent presence of a grass-dominated ecosystem throughout the middle Miocene.

In the late Miocene an important faunal change is recorded in the Mpesida Beds of Baringo (≈ 6 Ma) and farther north at Lothagam (< 7.9 Ma) with the introduction of porcupines, rabbits, and with turnover in hippos, giraffes, bovids, rhinos, and elephants (Leakey et al., 1996). The fauna has significant woodland elements (Cifelli et al., 1986; Leakey et al., 1996), but it also heralds the advent of a major bovid radiation in Africa (Vrba, 1995). Throughout the Miocene, the general impression of environments derived from fossil vertebrates ranges from forest to woodland, with a trend from more forested to more open environments. There is no strong evidence of Serengeti-style grasslands in eastern Africa during the Miocene.

The Miocene record from southern Africa is sparse, but several localities in southern Namibia are generally similar to those of eastern Africa (Hendey, 1978). However, more open environments than those of the early Miocene in eastern Africa may be indicated especially by the rodents, which include more hypsodont species than their east African counterparts (Flynn et al., 1983; Winkler, 1994), and in the dearth of arboreal primates in southern Africa. The younger locality of Arrisdrift is correlated with Maboko (Hendey, 1978), suggesting a middle Miocene age of approximately 15 Ma. The fauna includes suids, selenodont artiodactyls, an ochotonid, and other elements consistent with a riparian woodland. Given the early and middle Miocene faunal record of southern Namibia, the inception of the Namib desert postdates the middle Miocene. The fauna of Langebaanweg in the Cape Province of South Africa (not in the Namib Desert) is probably between 5 and 4 Ma and includes the earliest record of groove-toothed rats of the grass-eating muroid subfamily Otomyinae (Pocock, 1976; Jacobs, 1985), which, along with other taxa and evidence of fires, suggests an open environment in southern Africa at that time (Hendey, 1982).

STABLE ISOTOPES

Isotopic data relevant to the development of grass-dominated ecosystems in Africa are derived primarily from middle Miocene to Pliocene sites in the rift valleys of northern and western Kenya as

well as Tanzania. As discussed earlier, the site of Ft. Ternan (13.9 to 14.0 Ma) in western Kenya has been the focus of a number of paleoecological studies. Interest in Fort Ternan was originally largely generated by the interpretation that specimens of *Kenyapithecus* Leakey recovered from the locality were central to understanding the evolution of hominids (Leakey, 1967; Simons, 1963). As *Kenyapithecus* was considered to be a hominid, there followed the implication of bipedality, which characterizes the family, and therefore of grasslands, in which bipedality was hypothesized to have evolved.

Despite the interpretation of some plant macrofossils at the site as C_4 grasses (Dugas & Retallack, 1993), carbon isotopic analysis of paleosol carbonate and associated organic matter did not yield isotopic values consistent with C_4 vegetation (Cerling et al., 1991). Isotopic values were so depleted that Cerling et al. (1991) speculated that closed canopy conditions may have prevailed during formation of the paleosols. Subsequent analyses of fossil herbivore enamel from Fort Ternan indicated diets comprised of essentially pure C_3 plants (Cerling et al., 1997a).

Based on existing isotopic data at the time, Cerling (1992) concluded from analyses of paleosol carbonates collected from a number of hominid localities in Kenya and Tanzania that the proportion of C_4 biomass in East African ecosystems increased gradually over the last 10 Ma, culminating in pure C_4 savanna grasslands during the middle Pleistocene. He noted that the earliest evidence for C_4 plants was from paleosol carbonates collected from Ngeringerowa (9.4 Ma), in the Tugen Hills, which yielded isotopic values indicating $\approx 20\%$ C_4 biomass.

An isotopic study focusing on paleosol carbonates and associated organic matter from the Tugen Hills succession in the Kenya rift valley indicates that heterogeneous mixed C_3/C_4 habitats characterized this portion of the rift valley over the last 15.5 myr (Kingston et al., 1994). These isotopic data record habitats with predominantly C_3 vegetation (on average $> 65\%$) and suggest that C_4 grasses at no time dominated this portion of the rift valley during the Neogene. Associated paleosol organic matter from the Tugen Hills indicate a minor C_4 component until sometime between 8.5 and 6.5 Ma when there is an increase in paleosols yielding C_4 organic components. The carbon isotopic composition of fossil herbivore enamel from the Tugen Hills suggests that C_4 grasses were a minor dietary component at 15.3 Ma, but that there was a significant shift to a reliance on C_4 plants in addition to C_3

vegetation as a primary dietary resource sometime between 8.5 and 6.5 Ma (Kingston, 1992; Morgan et al., 1994).

Preliminary studies of the carbon isotopic composition in mammalian tooth enamel from Lothagam (\approx 7.9 to 3.7 Ma) and the somewhat older Namurungule Formation in the Samburu Hills of Kenya indicate mixed C_3/C_4 and exclusive C_4 diets throughout these horizons (Leakey et al., 1996). Published data relating to the chronology of the Namurungule Formation is limited, but radiometric dates on bracketing lavas (Matsuda et al., 1984) indicate that the sediments are between 13 and 7 Ma. A fossiliferous horizon within the Namurungule Formation, which has yielded a hominoid maxilla, has been dated to 9.5 Ma (Sawada et al., 1997, 1998), but the stratigraphic position of analyzed enamel relative to the dated horizon is unknown. Cerling et al. (1997b) interpreted tooth enamel carbon isotope data from sites in western Kenya, the Turkana basin, the Baringo Basin, and the Suguta depression as indicating a shift from C_3 -dominated to C_4 -dominated diet in equids and elephantids between \approx 8 and 7 Ma.

Stable carbon isotopic values of paleosol carbonate collected from the upper Baynunah Formation in Abu Dhabi (8–6 Ma) record the presence of both C_3 and C_4 vegetation at the time during which the soils formed (Kingston, in press). Lateral variability in the $\delta^{13}C$ of pedogenic carbonate implies a heterogeneous environment, roughly analogous to what would be expected in a modern grassy woodland habitat. None of the paleosol carbonates analyzed yielded $\delta^{13}C$ values indicative of open grassland. While an analysis of 34 Baynunah enamel specimens representing five herbivore families indicates that both C_3 and C_4 plants were available for consumption, there appears to be a heavy reliance on C_4 grasses with a significant number of taxa falling within the isotopic niche occupied by committed grazers. The interpretation is that the paleosol carbonates formed in more wooded environments flanking a river system, while many of the herbivores grazed in more open grassland or wooded grassland distal to the channel.

Analyses of terrestrial fauna, flora, and lithofacies from a limited number of Tertiary sites in the Arabian Peninsula (summarized in Kingston & Hill, in press) suggest that this region may have supported forested habitats in the Eocene and Oligocene. Paleoenvironmental data from early to middle Miocene sequences in eastern Saudi Arabia and part of western Abu Dhabi indicate more open habitats with limited closed habitat areas, possibly along river or lake margins.

AUSTRALIA

SUMMARY

The continent of Australia covers a wide latitudinal range from about 38°S to 11°S, with climates supporting tropical, subtropical, arid, and temperate vegetation. The interior is vast, and grass-dominated environments are widespread, covering a large area of the continent (Fig. 1). Savanna woodland and low tree and shrub savannas range across the central portion of the continent, except in the most interior region, which is desert (Cole, 1986). Savanna variants also occur in the northern and northeastern part of the country.

The earliest record of grass from Australia is in a middle Eocene pollen flora from the western part of the continent (Frakes & Vickers-Rich, 1991; Fig. 6). In southern Australia, around the Eocene-Oligocene transition, there is a decline in species richness among forest pollen taxa, possibly indicating cooling climate (Kemp, 1978; MacPhail et al., 1994). A major change in vegetation takes place beginning around 14 Ma when samples show an increase in charcoal and Asteraceae pollen with minor increases in grass, indicating a change to drier, more open, sclerophyll forest (Martin, 1990a). In eastern Australia, at approximately 4.5 Ma there is a brief resurgence of closed, wet forest followed by an abundance of grass, other herbaceous pollen, and charcoal, indicating open grass-dominated environments (Martin, 1981, 1990a; MacPhail, 1996).

The paleofauna of Australia is unique, dominated by marsupials, and lacks placental ungulates. Faunas prior to the middle Miocene are interpreted as representing forested environments. During the middle Miocene, familial and generic diversity decreases, and by the late Miocene hypsodont wombats are present. Arboreally adapted species decline throughout the Miocene, and grazing kangaroos are present by the early Pliocene.

There are no relevant stable carbon isotope data from Australia.

PALEOBOTANY

Australian pollen floras, particularly from the eastern and southern parts of the continent, provide a regional sample of vegetation change throughout the Tertiary. Macrofossil assemblages are uncommon except in the Eocene (Christophel, 1981; Greenwood, 1994). As a result of the uneven geographic distribution of paleobotanical sites, vegetation history for the arid interior region of the continent is relatively poorly known.

Eocene macro- and microfloras are uniformly in-

Australia

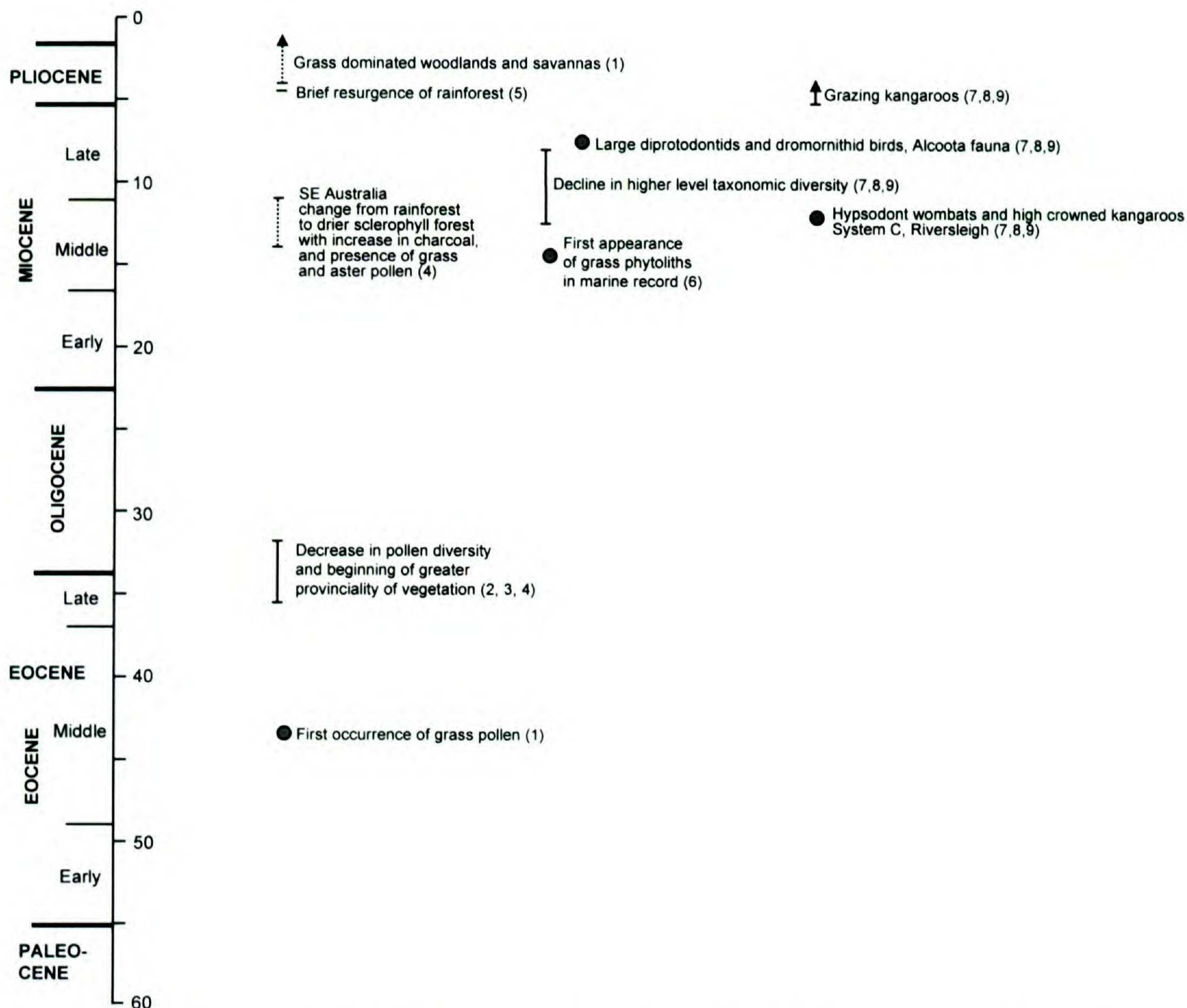


Figure 6. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in Australia. Symbols as in Figures 2 and 5. Sources: (1) Martin (1994), (2) MacPhail (1994), (3) Archer et al. (1995), (4) Kemp (1978), (5) Martin (1990a), (6) Locker & Martini (1986), (7) Archer et al. (1994a), (8) Archer et al. (1994b), (9) Archer et al. (1995).

dicative of tropical or closed forest (Kemp, 1978). The hallmark of Australian palynofloras from the late Eocene through the middle Miocene is the presence of *Nothofagus* pollen, most significantly, *Nothofagus* subg. *Brassospora* Philipson & Philipson [formerly, *N. brassii*-type, a fossil taxon with extant species in New Guinea, New Caledonia, and the New Hebrides (Martin, 1981; Kershaw et al., 1994)]. *Nothofagus* subg. *Brassospora* pollen becomes abundant in the late Eocene and indicates cool, rainforest vegetation (Kemp, 1978; Martin, 1990a; Archer et al., 1995). Diversity decline in southern Australia between the middle and late Eo-

cene may indicate cooling (Kemp, 1978), and the spread of *Nothofagus* subg. *Brassospora* is taken to indicate a change from megathermal rainforest in the early Eocene to mesothermal rainforest in the middle to late Eocene (MacPhail et al., 1994). Early to late middle Eocene southern Australian plant macrofossils also indicate forest conditions, but document local floristic variations in space and time not clearly evident from pollen assemblages (Christophel, 1981, 1994, 1995; Greenwood, 1994).

Oligocene to early Miocene macrofossils from Tasmania document the presence of rainforest containing Podocarpaceae, *Nothofagus* spp., Protea-

ceae spp., and other diverse angiosperms. Affinities lie with the lower montane rainforests of New Guinea and northernmost montane forests of New South Wales (Carpenter et al., 1994). Oligocene palynofloras are restricted to the southeastern margin of the continent and Tasmania. They indicate lower diversity than Eocene floras and further cooling in southern Australia at the Eocene-Oligocene transition (MacPhail et al., 1994). Coal and some forest taxa indicate wet conditions, although probably not as wet as the Eocene (Kemp, 1978; Greenwood, 1994; Archer et al., 1995). Physiognomically, Oligocene plant macrofloras show evidence of environments drier than the Eocene by the presence of smaller, sclerophyllous leaves (Christophel, 1995). In addition, the mesic indicators of the Eocene are replaced in Oligocene to Miocene macrofloras by such taxa as *Eucalyptus* L'Hér., *Banksia* L. f. (Proteaceae), *Allocasuarina* L. Johnson, and *Casuarina*, which have extant relatives in drier environments (Christophel, 1995). Grass pollen is present in western Australia by the late middle Eocene (≈ 40 Ma, Frakes & Vickers-Rich, 1991, and references therein) but is extremely rare until at least the early Miocene, when it is present in small amounts, constituting not more than approximately 10% of assemblages at inland sites in eastern Australia (Kershaw et al., 1994).

A palynoflora from the late Oligocene to early Miocene Namba Formation in central Australia was originally reported to contain abundant grass pollen and interpreted as an open, grass-dominated environment (Callen & Tedford, 1976; discussed in Archer et al., 1995). In a reanalysis, Martin (1990b) discovered that much of the grass-like pollen is in the family Restionaceae rather than Poaceae. Also present in the assemblages were algae (*Botryococcus* Kützing and *Pediastrum* Meyen), Cyperaceae, and Sparganiaceae, all indicators of a wetland environment and leading to the conclusion that the site was a marsh. Napperby and Hale River from the arid interior of Australia are tentatively dated to middle Eocene on the basis of palynological indicator fossils (Truswell & Harris, 1982). Both pollen floras contain taxa not usually found until the Neogene, including Cyperaceae, *Callitris* Vent., and *Micrantheum* Desf. at Napperby, and as much as 2% grass pollen at Hale River. The remainder of the pollen assemblages have more typical arboreal taxa, such as *Nothofagus* subg. *Brassospora*, *Podocarpus* L'Hér. ex Pers., and *Casuarina* (Truswell & Harris, 1982). The vegetation reconstruction is forest with grass growing in small clearings (Truswell & Harris, 1982). Paleogene pollen assemblages of New Zealand compare favorably with veg-

etation reconstructions for southern Australia including the dominance of *Nothofagus* subg. *Brassospora* from the latest Eocene to early Miocene (Pocknall, 1989, 1990).

A major change in pollen floras occurs in the middle to late Miocene, beginning about 13 Ma, and documented primarily in southeastern Australia. *Nothofagus* subg. *Brassospora* disappears, Myrtaceae increase (including both dry and wet-adapted *Eucalyptus* and other rainforest taxa in this family), and grass and Asteraceae pollen occur in low percentages (Martin, 1990a; Kershaw et al., 1994). At the same time, the occurrence of charcoal in pollen samples begins to increase. Marine records document the first appearance of grass phytoliths at 14.4 Ma (Locker & Martini, 1986; Martin, 1990a). The changes in pollen and charcoal indicate tall, open, wet sclerophyll forest where eucalypts form the canopy and rainforest taxa grow in the understory (Martin, 1990a; Kershaw et al., 1994). The change to drier sclerophyll forest during the middle to late Miocene in southeastern Australia indicates increased provincialism among plant communities. Although there is some evidence for differences among regional floras during the early Tertiary, by the middle to late Miocene increasing aridity resulted in greater distinctions between northern wet, interior dry, and southern cool wet regions (Martin, 1990a; Christophel, 1995).

At about 4.5 Ma, a short-lived resurgence of rainforest taxa (including *Nothofagus* spp. other than *Nothofagus* subg. *Brassospora*) is indicated in pollen records of the southeast (MacPhail, 1996). After this, a substantial increase in the relative percentages of Asteraceae and Poaceae pollen concomitant with high charcoal counts and a dramatic increase in grass phytoliths in marine cores indicate a change to open woodlands, savannas, and grasslands (Locker & Martini, 1986; Martin, 1981, 1990a).

PALEOFAUNA

The sporadic fossil mammal record of Australia, much of which is only loosely constrained temporally, is summarized in Archer et al. (1994a, b, 1995), Vickers-Rich et al. (1991), and Woodburne et al. (1994). Due to its long zoogeographic isolation, the composition of its Cretaceous and early Tertiary mammal fauna, and the dynamics among the early Tertiary fauna as the continent assumed its rigid isolation, Australia has a distinct marsupial-dominated fauna, lacking placental ungulates except those introduced by humans for agricultural purposes. Browsing and grazing roles throughout

the Tertiary, played most conspicuously by ungulates on other continents, are filled mostly by larger kangaroos and wombats in Australia. The dental and skeletal modifications of these marsupials are different from those of placental ungulates; thus, the criteria used in interpreting environmental structure from morphology are somewhat different. Studies of morphology and diet with respect to Australian herbivores and functional similarities between kangaroos and ungulates include Janis (1990a, b), Sanson (1989, 1991), and Wright et al. (1991). The development of high-crowned teeth remains a reliable indicator of abrasive diet, often associated with a diet of grass. However, Janis (1990a) determined that most functional differences in teeth and skulls between kangaroos and ungulates are related to food handling and tooth occlusion. Moreover, Janis (1988) suggested that large kangaroos without markedly hypsodont teeth, but with other dental adaptations (Janis, 1990c), might facilitate feeding by selecting and manipulating food with their forelimbs, discarding grit and dust before ingestion.

Prior to the late Oligocene, the mammalian fauna is poorly known. The Eocene Tingamarra fauna (Godthelp et al., 1992; see Woodburne & Case, 1996, for a discussion of problems with the dating) contains about a dozen taxa of mammals recovered with frogs, turtles, crocodiles, and birds. All of the mammals are small and none appears to exhibit folivorous or other herbivorous adaptations. The locality is interpreted as representing a swamp or shallow lake. The record becomes better in the late Oligocene and early Miocene, with faunas best known from South Australia where chronology of the earlier faunas is constrained by paleomagnetic stratigraphy (Woodburne et al., 1994), and from the Riversleigh area (the Low Lyon fauna and others in stratigraphically designated systems A and B) in Queensland, farther to the north. As summarized by Archer et al. (1995), the South Australia sites (Ditjimanka, Ngapakaldi, and Ngama of the Etadunna Formation) produce a mammalian fauna less diverse than correlated faunas from Riversleigh. The interpretation is that of a relatively open, wet forest community. The overlying Kutjamarpu fauna has some taxonomic similarity to system B and C faunas from Riversleigh. None of the South Australia sites is interpreted as having significant grassland habitat. At Riversleigh, faunas are more diverse and are interpreted to represent rainforest communities. No high-crowned grazers are known from the early Miocene, although there are terrestrial browsers (macropodids and diprotodontids), as

well as arboreal folivores, frugivores, and omnivores.

Middle Miocene faunas from Australia include the Bullock Creek fauna in the Northern Territory and those from System C (Dwornamor, Ringtail, Henk's Hollow) in the Riversleigh area, where there is a reduction in mammalian families and genera and turnover in species between System B and System C. Herbivorous mammals are abundant, suggesting the presence of rainforest, but not open forests. The presence of frog species whose modern relatives produce bubble nests suggests that the temperature remained below 20°C, when such nests would be utilized. Within the lower portion of System C, generic diversity in arboreal pseudocheirid possums declines. In the upper levels of System C, rainforest frogs are rare. Wombats of System B are low crowned. In contrast, only hypsodont wombats are present in most of System C assemblages. At the Encore Site, from the uppermost System C (late Miocene or possibly late middle Miocene), only rootless (hypsodont) wombats are present.

The Bullock Creek fauna of the Northern Territory has relatively fewer arboreal species, and it is dominated by a large species of the diprotodontid *Neohelos* Stirton, which also occurs in upper System C at Riversleigh. The genus *Neohelos* shows an increase in size through the Miocene. A rare, relatively high-crowned kangaroo is the only evidence of grazing, although abundant terrestrial browsers and reduced arboreal species are consistent with a more open habitat than that at Riversleigh.

The Alcoota fauna of the late Miocene (perhaps 7–8 Ma) in the Northern Territory is dominated by large diprotodontids and dromornithid birds, such as *Dromornis stirtoni* Rich, one of the largest known birds in the world. Arboreal mammals are extremely scarce. Macropodids and diprotodontids have dentitions suggestive of browsing. The Northern Territory site of Ongeva is younger, possibly 5–6 Ma, but is similar to the Alcoota. The mammalian fossil record of the Pliocene suggests further decrease in forested area and aridification of the central portion of the continent.

Australia's unique dry country fauna, derived from equally curious endemic rainforest antecedents (without the addition of ungulates from other continents), is known as the "Green Cradle Concept" (Archer et al., 1994b). The decline in species with arboreal adaptation and the increase in species adapted to more open habitats occurred through the Miocene, with the early Pliocene and younger times being characterized by grazing kangaroos.

DISCUSSION AND CONCLUSIONS

At the outset of this review we posed three fundamental questions: When do grass-dominated ecosystems first appear? Do grass-dominated ecosystems become established synchronously around the world? Is the evidence from paleobotanical, vertebrate, and isotopic data concordant? It has become clear that the origin and spread of grass-dominated ecosystems is synonymous with the evolutionary history of the Poaceae itself, and that the paleobotanical, paleofaunal, and isotopic records, individually and in concert, elucidate the major phases in that history, even if only in the most general way.

The major phases in the origin of grass-dominated ecosystems appear to have been: (1) latest Cretaceous or early Tertiary origin of Poaceae; (2) the opening of Paleocene and Eocene forested environments in the early to middle Tertiary; (3) an increase in the abundance of C_3 grasses during the middle Tertiary; (4) the origin of C_4 grasses in the middle Miocene; and (5) the spread of C_4 grass-dominated ecosystems at the expense of C_3 grasses in the late Miocene (Fig. 7).

Phylogenetic analyses of living grasses based on molecular, morphological, and anatomical characters are concordant in placing Joinvilleaceae as the sister group to Poaceae (Kellogg & Linder, 1995; Duvall & Morton, 1996; Kellogg, 1998; Soreng & Davis, 1998). Bambusoideae, Pooideae, and Oryzoideae are primitive subfamilies (which may form a clade) and must have originated early in the history of Poaceae, but their relative positions are unresolved (Renvoize & Clayton, 1992; Duvall & Morton, 1996; Kellogg, 1998). The remaining subfamilies, all of which include C_4 photosynthesizers, resulted from later radiations within the family, consistent with their younger fossil record. Resolution of the early evolution of grasses must eventually be understood through macrofossils. However, with the exception of the rare North American Eocene and Oligocene specimens, unequivocal early Tertiary grass macrofossils are currently lacking (Thomasson, 1987).

Grasses are predominately wind pollinated and able to survive seasonal climates, leading to reasonable speculation that grasses first evolved in an open environment (Stebbins, 1987), near a forest margin (Renvoize & Clayton, 1992), or in warm-temperate, subtropical, tropical dry, or seasonally dry, environments (Crepet & Feldman, 1991; Soreng & Davis, 1998). The consistent presence of *Monoporites annulatus* pollen during the early Tertiary in northern South America (Germeraad, 1968) and western Africa (Adegoke et al., 1978; Salard-

Cheboldaeff, 1979, 1981) indicates that diversification may have taken place in the tropics at that time. Romero (1993) hypothesized that South American chacoan woodlands, which today have a significant grass ground cover, may have originated in the Oligocene, based on palynological assemblages. Paleogene paleobotanical records from the Northern Hemisphere indicate that grass was not a significant ground cover (Leopold & MacGinitie, 1972; Frederiksen, 1991; Leopold et al., 1992).

Clear evidence of widespread grass-dominated ecosystems does not occur until the early to middle Miocene, albeit with the intriguing possibility that grasses played a significant role in Paleogene communities of South America and West Africa. In the Northern Hemisphere, grass does not appear dominant by any criterion until the Miocene, during which time all five subfamilies of the Poaceae, and both C_3 and C_4 photosynthetic pathways, are present in North America, as documented by plant macrofossils. However, only in the late Miocene does a distribution of C_4 grasslands similar to that of the present day become established, as brought to light by isotopic analyses.

Turning to the relevance of the paleofaunal record, mammalian herbivores can be characterized by the structure of their teeth, which in turn can be correlated with ecological and environmental criteria related to the diet of the animal. Such relationships allow the ecological history of communities, as well as taxonomic composition, to be evaluated through time. Although some multituberculates occurred in the Mesozoic, the origins of most mammalian herbivore diversifications were Paleocene and Eocene in age. During that interval, forests were widespread. Mammalian herbivores were predominately low-crowned folivores and frugivores. Browsers having teeth with distinct ridges (lophodont and selenodont) became increasingly more common toward the end of the Eocene and Oligocene. Grazing mammals elaborated on those patterns, especially in the Miocene, by increasing crown height.

Jernvall et al. (1996) evaluated mammalian herbivore molar patterns in the Eocene of North America and Eurasia relative to molar patterns in the Miocene. Their approach was focused on the morphology of the crown of second molars as distinct ecological types independent of phylogeny and without regard to taxonomy. Twenty-eight crown types were identified in early Tertiary perissodactyls, artiodactyls, and primitive ungulates, or condylarths. Of those basic crown types, only eight are currently found in extant perissodactyls and artiodactyls. In the Eocene, the basic crown types were

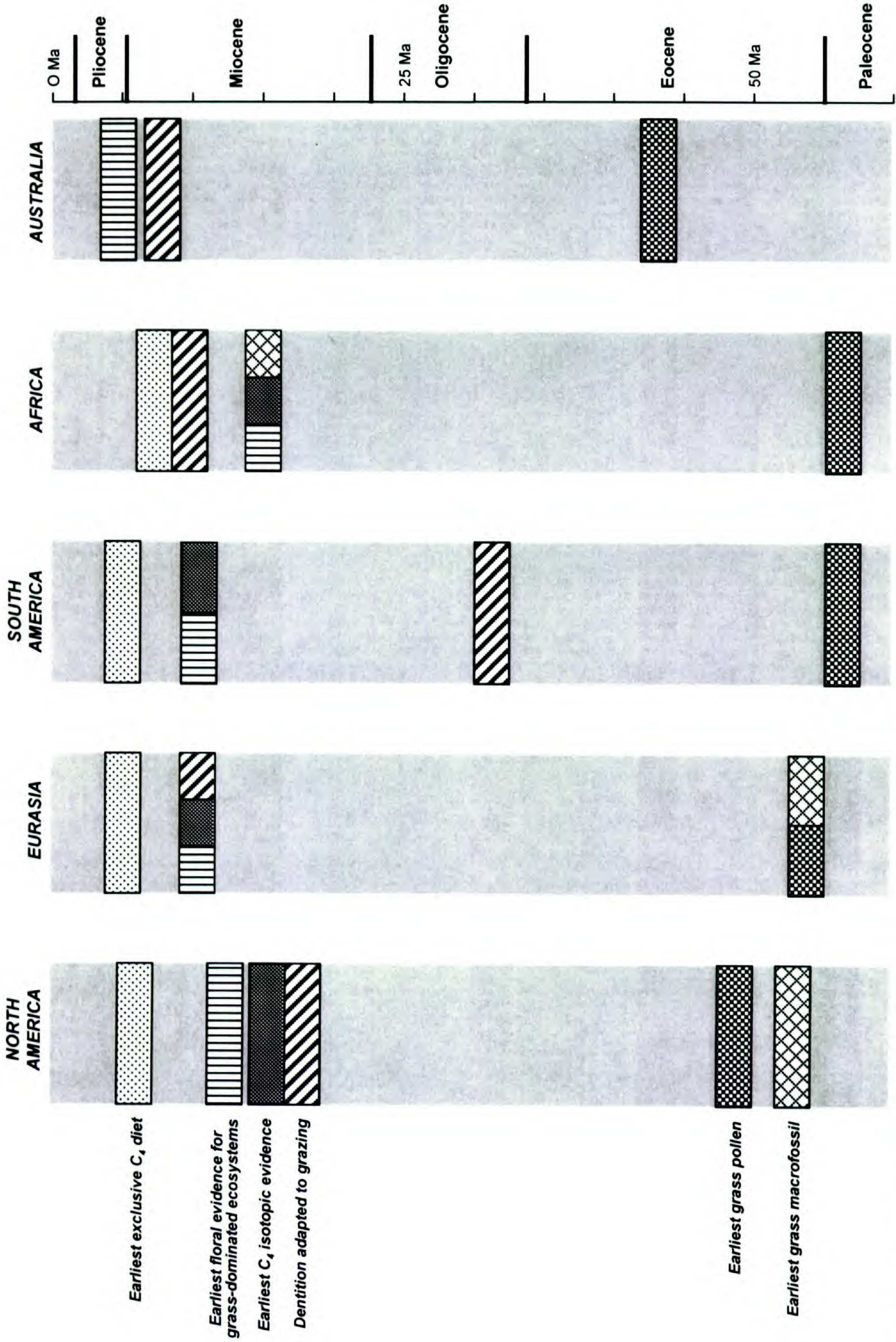


Figure 7. Generalized summary of the establishment of grass-dominated ecosystems during the Tertiary in North America, Eurasia, South America, Africa, and Australia based on paleobotanical, paleofaunal, and isotopic evidence. Patterns defined on the left apply to all columns; their order of appearance may vary.

possessed by only a few genera each, suggesting that in the early Tertiary radiation of herbivorous mammals, morphological diversification matched taxonomic diversification. Morphological diversity in crown types increased from the early to the late Eocene, followed by a decline in morphological diversity of basic crown types during the Oligocene (see also Janis, 1997).

On the other hand, Jernvall et al. (1996) found that herbivorous ungulates of the Miocene presented a very different pattern from the herbivores of the early Tertiary. Taxonomic diversification of ungulates in the Miocene was at the familial level or lower and did not lead to a similar diversity of crown types as was the case in the early Tertiary. After the Eocene, ungulate dental morphology comprised fewer basic crown types, but in the remaining types the development of lophs and ridges increased. Morphological differentiation among remaining lophodont crown types became greater, even though the total number of crown types was less than in the early Tertiary. The recurrent trend was to increase lophs in teeth, often accompanied by increased crown height, both traits related to the processing of tough, fibrous vegetation of relatively low nutritive value (Jernvall et al., 1996). Assuming a similar availability of resources, the resultant morphological disparity within a few basic crown types probably reflects greater partitioning of resources among Miocene ungulates and perhaps other taxa, as compared to the adaptive radiation of early Tertiary herbivores. The trend toward lophodonty is seen in North America, Europe, and Asia, although the basic morphological types on which the lophodont patterns are built vary among these regions, reflecting the taxon-independent ecological significance of the morphological trends.

Pascual and Ortiz Jaureguizar (1990) also noted that early Tertiary taxa are diverse but show fewer extremes of morphological differentiation than later in the Tertiary when morphologies became more divergent. In Australia, the Miocene record might show a comparable pattern with communities later in the Tertiary having fewer higher-level taxa than earlier (Archer et al., 1995). On every continent, more or less independently from other continents, the herbivore fauna was uniquely adapting along with global and regional climatic conditions that affected vegetation, and hence the food resource, which included substantial grass at some time during the middle Tertiary.

Thus, the trend toward lophodonty became prevalent in the late Eocene, affecting different taxa in different regions. In North America, Europe, and Asia, primarily perissodactyls and artiodactyls

among larger mammals became lophodont. In South America, it was mainly notoungulates and other endemic ungulate groups. In Australia, marsupials eventually become lophodont. In Africa, although the record is poor and not representative for most of the continent, hyracoids exhibited the trend. In fact, we would predict that if the record for the Oligocene were to become better known, especially from northwestern Africa, diverse lophodont high-crowned hyraxes, perhaps elephant shrews, would be discovered. The patterns on different continents, so far as they can be compared, emphasize the global ecological significance of these trends. However, the differences in the starting points for each continent also help to explain some other profound biogeographic differences: such as why equids exhibit their tremendous evolutionary radiation of high-crowned forms primarily in North America, which feeds minor radiations in Eurasia through dispersal events; or why bovids are prevalent today in Africa but never had a comparable diversity in North America, an issue of relevance when evaluating the adaptive patterns and ecological deployment of bovids versus equids (see also Janis, 1976).

The importance of increased lophodonty and hypsodonty in interpreting the origin of grass-dominated ecosystems is that the earliest common occurrence of hypsodonty is taken to reflect the origin of widespread grass-dominated ecosystems because grazers generally have high-crowned teeth. The obverse of the adaptation of high-crowned grazers to a diet of grass is the protective mechanisms of grass that are induced by grazing. Initial experiments showed that silica content in Serengeti grass species increased in response to grazing intensity both in the field and in laboratory leaf-clipping experiments and that silica content was highest for grasses from the most intensely grazed areas (McNaughton & Tarrants, 1983; McNaughton et al., 1985). These data supported the hypothesis that silica production is an inducible defense against herbivory (McNaughton & Tarrants, 1983) and provided supporting data for the coevolution of grasses and grazers. However, more recent studies, reviewed by Vicari and Bazely (1993), indicate a more complicated relationship. Silica as a defense mechanism in grasses appears most effective against invertebrate herbivores; its protective role against vertebrate herbivores is inconclusive, and whether silica production can be induced in individual plants is questionable. Nevertheless, the enhanced silica content in grasses generally suggests that its effects were relevant to grazers on an evolutionary time scale.

The complexity of the relationship among ver-

tebrate and invertebrate herbivores and grasses notwithstanding, the North American record with its radiation of high-crowned equines and corresponding record of grass macrofossils and isotope studies stands out as unique. Plant macrofossils present in North America, but not documented on other continents, provide evidence of grass species diversity and evolution during the middle to late Miocene, concomitant with the well-documented contemporary evolutionary radiation of hypsodont mammals, particularly horses.

Although it seems reasonable that grasses may have been a dietary component of some early Tertiary mammals, faunal evidence indicates that large expanses of grass-dominated environments only occurred significantly later than the early Tertiary in most areas. However, morphology indicative of grazing, and therefore suggestive of a grass-dominated ecosystem, appears in South America by the Eocene-Oligocene boundary, prior to the occurrence of grazing morphology elsewhere. Moreover, grazing adaptations persist into the late Oligocene along with indications of aridity at the locality of Salla, Bolivia. Thereafter, a case can be made for grazing ungulates throughout the remainder of the Cenozoic in South America. This pattern is accepted by us as indicating that the coevolution of grazers and grasses, and the establishment of grass-dominated ecosystems, occurred prior to the early Miocene in South America.

In the Northern Hemisphere during the Oligocene, browsing mammals diversify, but there is no clear evidence of grazing animals at that time, consistent with the paleobotanical record, which indicates a lack of grassy ground cover. Grazing and mixed-feeding mammals characterize the Miocene in North America. This pattern, in contrast to that of South America, is taken to mean that coevolution of grasses and grazers did not occur prior to the early Miocene in North America, and by extension, that grass-dominated ecosystems developed earlier in South America, although the paleobotanical record there is relatively poor.

The relevance of geochemical investigations to the origin of grass-dominated ecosystems is in identifying the isotopic signal of C_4 grasses, as opposed to that of C_3 plants. Because C_4 grasses are restricted to open terrestrial habitats and do not include forest or aquatic species, a C_4 isotopic signal clearly indicates broad grass cover and by extension, grass-dominated ecosystems. The application of isotopic techniques to the study of grassland evolution, with the consequent definition of the late Miocene spread of C_4 grasses, is a significant advance in paleoecological studies. It does not, how-

ever, signify the initial development of grass-dominated ecosystems.

Because most plants use the C_3 photosynthetic pathway and the C_4 pathway is a supplement to basic C_3 biochemistry, C_3 photosynthesis is considered the primitive state for grasses. Although grass is known from the early Tertiary, the earliest carbon isotopic records tentatively interpreted as having a C_4 component are approximately 15 Ma (Kingston et al., 1994; Latorre et al., 1997). Furthermore, the earliest plant macrofossil with Kranz (C_4) anatomy is dated to about 12.5 Ma (Nambudiri et al., 1978; Whistler & Burbank, 1992). This record suggests that C_4 grasses were present during the middle Miocene spread of grass-dominated ecosystems, even though they did not constitute a significant portion of grass biomass until later (Cerling et al., 1998). It further suggests that the co-evolution of ungulates and grass-dominated ecosystems, accepting that it is a real phenomenon, originally involved C_3 grass. This is not an unreasonable conclusion considering that C_3 grasslands occur today at higher altitudes and latitudes, such as the northern Great Plains, and that C_3 grasses are more nutritious than C_4 grasses (Akin & Burdick, 1975; Wilson & Hacker, 1987).

The timing of the shift from C_3 to C_4 grass domination in lower latitudes is striking. Between 9 and 4 Ma, an expansion of C_4 biomass has been documented in North America, South America, East Africa, and Pakistan, although the transition may have taken place in a shorter interval in some regions (Quade et al., 1989a; Cerling et al., 1997b, 1998). This major ecological shift signifies a transformation in species composition that was undetected before the application of carbon isotope studies.

C_4 grasses are characteristic of seasonal, arid, and warm environments, and they do better than C_3 plants under lower atmospheric CO_2 conditions (< 400 ppmv, Ehleringer, 1991). These attributes suggest either climatic factors, or atmospheric composition, or both, controlled the spread and distribution of C_4 grass in the late Miocene. Within the scale of this review, it suggests the establishment of essentially modern seasonality and rainfall patterns in the late Miocene. In addition, higher ratios of atmospheric CO_2/O_2 during the early to middle Miocene may have allowed C_3 grasses to occupy the niche of C_4 grasses today forming extensive grass-dominated ecosystems in tropical regions.

As C_4 grasses became more widely distributed and abundant, displacing C_3 vegetation, they became the primary diet of some ungulates. In North America, the dietary shift began in the southern

Great Plains around 7 Ma and in the central Plains by about 4 Ma (Wang et al., 1994; Cerling et al., 1998). Concomitant with this dietary change is a substantial decline in equid diversity from nine to three genera (MacFadden, 1992; Cerling et al., 1998). One explanation for this species decline is a decrease in the woody vegetation and an increase in treeless grassland, thus limiting food resources needed to support a high diversity of ungulates. That explanation retains merit because diversity of browsing and mixed-feeding species declines in the North American Miocene. However, the isotope data emphasize the intriguing possibility that the change in grass species composition, from predominantly C_3 to predominantly C_4 species, could have been a causal factor in the equid diversity decline (Cerling et al., 1998). C_3 grasses have more digestible matter than C_4 grasses due largely to anatomical attributes of C_4 grasses (especially of the cell walls in bundle sheath parenchyma and vascular tissue; Akin & Burdick, 1975; Akin et al., 1983; Wilson & Hacker, 1987; Wilson & Hattersley, 1989). The decline in ungulate diversity at the end of the Miocene paralleled the spread of less nutritious grass over much of their range.

On the other hand, decrease in nutritive value of C_4 plants relative to C_3 plants may be compensated by complex interactions between herbivores and their environments. The Serengeti, a C_4 grass-dominated ecosystem, supports the most diverse and dense ungulate fauna on earth today. Although Serengeti grazers have been shown to be sensitive to food quality, differential feeding and migration by various ungulate species enables them to coexist in this grass-dominated environment (McNaughton et al., 1985). Grazing bovids appear to have increased with the origin of C_4 grass-dominated ecosystems in Africa.

The role of grass-dominated ecosystems in human evolution has long been debated. The paleobotanical record of Africa derives special significance because the development of grass-dominated ecosystems has long been considered to play a central role in the evolution of bipedality, the defining character of the human family. A traditional perception in paleoanthropology, informally referred to as the savanna hypothesis, is that as rainforests became restricted in distribution during the late Miocene, more seasonal and drier woodland and grassland habitats became more widespread. Many of the morphological and behavioral innovations documented in the fossil hominid record have been interpreted as adaptations to these more open habitats. Deciphering the timing and biogeographic distribution of the earliest grasslands in Africa is

therefore critical in assessing whether the development of grass-dominated biomes, or more specifically C_4 grass-dominated biomes (Cerling et al., 1997b), was a driving force in human evolution.

East African early and middle Miocene localities represent a variety of habitats, most of which appear to be forested, but one of which (Fort Ternan, 14 Ma) contains significant grass pollen and macrofossils. However, throughout most of the East African Miocene there is no clear record of a consistent grass-dominated ecosystem, but rather a spatial and temporal pattern of environmental heterogeneity. The pollen and charred grass cuticle record from the Niger delta clearly signifies the possibility of a grass-dominated ecosystem in western Africa by about 16 Ma, peaking in the late Miocene (about 7 Ma). However, vertebrate fossils of the relevant age, including hominoids, are unknown in western Africa. If hominids evolved in the late Miocene of East Africa, there is as yet no firm evidence to link their origins with the earlier development of grass-dominated ecosystems.

Overall, the plant, vertebrate, and isotopic records, where they occur together, are concordant with respect to the origin of grass-dominated ecosystems. However, the records are of varying detail, and severely limited by the quality and distribution of localities for plants, animals, and isotopes. Moreover, they are less definitive and less constraining than is desirable. Nevertheless, the series of five major phases in the origin of grass-dominated ecosystems listed at the beginning of this section is derived from these records, which reflect not only origins but change through time. Perhaps a sixth major stage should be added in closing: The development of agricultural grasslands. All that we know of the geological history of grass-dominated ecosystems instructs us that the processes of ecosystem evolution are profoundly influenced by large-scale changes beyond human control. However, the sixth stage in the origin of grass-dominated ecosystems, in which we find ourselves now, is unique because there are aspects, such as the maintenance of floral and faunal diversity, that can certainly be influenced by considered management.

Domesticated grass species include both C_3 , e.g., wheat, and C_4 , e.g., corn, physiologies naturally adapted for life in distinct environmental settings. How domesticated and genetically engineered C_3 and C_4 grasses, or naturally occurring grasses for that matter, will be affected by the combined changes in temperature, rainfall, and pCO_2 that would likely be a part of a pCO_2 -caused climate change cannot be realistically predicted at this time (see discussion in Hattersley & Watson, 1992). But

we do know that grass physiology is sensitive to these factors, and changes in them can result in a rapid change in species distribution, as has been demonstrated for climate and grass communities at the terminal Pleistocene in North America (Kurtén & Anderson, 1980; Fredlund & Tieszen, 1997), and has been suggested to explain the patterns in the fossil and isotope records for the Tertiary. Thus, an increased understanding and deeper consideration of both modern and ancient grass-dominated ecosystems should help us anticipate species stress in response to global climate change, such as that predicted from human-induced increases in atmospheric $p\text{CO}_2$.

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